VARIATION IN GERMINATION RESPONSE TO TEMPERATURE AMONG COLLECTIONS OF THREE CONIFERS FROM THE MIXED WOOD FOREST

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ABSTRACT

White spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Mill.) BSP), and jack pine *(Pinus banksiana* Lamb.) are dominant conifer trees within the boreal forest. Rising CO_2 concentrations may create hotter and drier conditions in the Southern Boreal Forest of Canada, and have negative impacts on germination and regeneration of conifers. Conifers vary in their germination requirements and may have different responses to climate change. Experiments were conducted to access the germination potential, variability among collections, and to predict the ability of these conifers to germinate under future climatic conditions. Twelve collections of white spruce and black spruce and ten collections of jack pine seeds were collected from the Boreal Plain Ecozone of Saskatchewan. Seeds of all collections varied in their dormancy characteristics and dormancy breaking requirements because no single stratification or light treatment stimulated germination in all three species. Seed dormancy was greatest in white spruce and least in black spruce. Germination tests at 5, 10, 12.5, 15, 17.5, 20, 25, 30, and 35°C were used to develop thermal time models. Each species had unique temperatures for optimal germination ranging from 20°C in white spruce, 20-25°C in black spruce, and 25-30°C in jack pine. The speed of germination under similar temperature regimes was fastest for jack pine, intermediate for black spruce, and slowest for white spruce. The base temperature for white spruce decreased ($r=0.63$, $P=0.03$) with increasing June precipitation while that of jack pine tended to increase with latitude ($r=0.60$, $P=0.07$) and April precipitation ($r=0.58$, $P=0.08$). No environmental variables correlated with germination of black spruce. The Canadian Global Climate Model, version 2, with emission scenarios predicted future temperature and precipitation at the sites where seeds were collected. Using the base temperature for germination as a guideline, temperatures suitable for germination in the spring are predicted to advance by a few

weeks to a month and a half earlier with increased concentrations of CO_2. Moisture availability may, however, control seed germination at these sites. Overall, jack pine and black spruce might better adapt to increasing temperature because of their high germination temperatures (>30°C). Variation in most germination parameters existed among collections, suggesting this variability can be used to select seed sources for reforestation or assisted migration in a changing climate.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1.0 INTRODUCTION

Global climate change is an escalating concern because it may have numerous economic and ecological consequences in the future. By the end of the century, the global mean temperature is predicted to rise at an unprecedented rate, between 2 and 5ºC (Peters 1990, Wang et al. 1994). Many studies have attempted to simulate the effects of global warming on the Boreal Forests of Canada (Lenihan and Neilson 1994; Wang et al. 1994; Hogg and Hurdle 1995; Hogg and Schwarz 1997; Shugart et al. 2005), and the general consensus indicates that increases in atmospheric CO2 concentrations will lead to a drier and hotter climate in the Southern Boreal Forest of western Canada. Many studies predict that forest biomes will shift poleward as individual species track favorable climatic conditions, causing "retreating species" to become less competitive at their southern boundaries (Emanuel et al. 1985; Hansen et al. 2001; Goldblum and Rigg 2005. Climate change may cause a decade to century lag because of the long life cycle of conifer species and potential genetic constraints that limit their ability to respond to the selective pressures brought by rapid climate change (Etterson and Shaw 2001; Andalo 2004; Goldblum and Rigg 2005). Over the next 50-100 years, the geographic range of species in the boreal forest may shift approximately 300-500 km north (Stewart et al. 1998). The Boreal Plain Ecozone was chosen as the focus of this study because it represents the southern region of the boreal forest in Saskatchewan that is at risk of being replaced by grasslands under global warming (Sargent 1988; Rizzo and Wilken 1992).

Hogg and Schwarz (1997) reviewed several studies examining the effects of climate change on conifer regeneration in northern boreal and sub-arctic regions of Canada (e.g., Elliot

1979; Payette and Filion 1985). However, little attention has been placed on conifer regeneration in the southern boreal forest under future climate change scenarios, especially under increasing temperature (Hogg and Schwarz 1997). Climate change may significantly reduce the natural regeneration of conifer trees (Hogg and Schwarz 1997), and decrease the yield of commercial species in the southern boreal forest (Hogg and Hurdle 1995). Germination is the first and most environmentally dependent stage during forest regeneration (Li et al. 1994). Seed germination and dormancy characteristics under variable conditions are key to the regeneration success of these species under future climate. Seed germination will become increasingly important in natural and managed forest regeneration of boreal trees as climate change proceeds (Wang et al. 1994). Appropriate seedling selection is central to successful breeding programs and reforestation (Wang et al. 1994). Economic losses can occur from planting trees in altered provenances (Vaartaja 1959), and regeneration of conifers is important for stand maintenance (Hogg and Schwartz 1997). In the absence of regeneration in the southern boreal forest, conifer stands are prone to replacement by aspen (*Populus tremuloides* Michx) or grassland following fire and other disturbances (Schwarz and Wein 1992; Hogg and Hurdle 1995).

In an effort to expand knowledge in this area, the germination potential of white spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Mill.) BSP), and jack pine (*Pinus banksiana* Lamb.) was assessed under climate change scenarios. These species are the most important and widely used species for reforestation in Canada (Janas 1985). Considerable information is available on growth, development, distribution, dormancy, and germination of these species. The regeneration potential of these conifer species under future climatic conditions, plasticity in dormancy status, germination requirements, spatial variation, and local adaptation must be studied. Knowledge of such species-specific and site-specific characteristics

can help understand, predict, and direct the regeneration and succession processes of the boreal forest (Li et al. 1994).

Seed dormancy is a mechanism that ensures germination takes place at the right time to improve seedling survival (Fenner and Thompson 2005). When seed dormancy and germination requirements are viewed on a global scale, a spatial pattern from arctic to temperate and from temperate to tropical regions is revealed. Levins (1969) proposed dormancy is an adaptation to changing and uncertain environments more frequently in middle and high latitudes in North America. The prevailing climate has a strong effect on the degree of dormancy in seeds and dormancy may be associated with environmental heterogeneity (Angevine and Chabot 1979). As stated by Fenner and Thompson (2005): "the most strict requirements for dormancy breaking need not be found among species that experience the longest and most severe unfavorable periods". Therefore, seeds in arctic tundra may not have dormancy restrictions because they do not have periods of mild weather in which they may be 'tricked' into germinating prematurely. This area has a higher chance of continuous below freezing temperatures relative to temperate environments; therefore there is less need for a long period of dormancy (Levins 1969). Likewise, seeds of plants in tropical regions usually do not exhibit dormancy, because climatic conditions are often favorable year round. Enrique and Flores (2005) compiled germination data for 3164 species; seeds of 60% of the species were non-dormant and from frost-free and drought free environments. Seeds of most temperate zone plants exhibit some degree of dormancy (Bevington 1985). The range of dormancy usually depends on the provenance of seeds. Many studies have shown that northern seeds require shorter stratification periods and they germinate faster at lower temperatures relative to southern provenances (Mergen 1963; Fowler and Dwight 1964; Farmer 1971). For example, northern populations of redroot amaranth (*Amaranthus*

retroflexus L.) germinated at lower temperatures than southern populations (McWilliam et al. 1968). Similar patterns of germination also occur in paper birch (*Betula papyrifera* Marsh.) (Bevington 1985). White spruce, black spruce show some degree of conditional dormancy (Wang and Berjak 2000; http://www.na.fs.fed.us) while jack pine is usually considered non-dormant (Rudolph and Yeatman 1982).

Temperature is among the most influential environmental factors affecting germination of seeds. Thermal time models can be used to predict germination response to temperature. Several studies have illustrated the effectiveness of using thermal time models to predict germination in a variety of species including common lambsquarters (*Chenopodium album* L.), winterfat (*Eurotia lanata* (Pursh) Moq.), pearl millet (*Pennisetum glaucum* (L.) R. Br.), lentil (*Lens culinaris* Medik.), and many grasses (Ellis and Barrett 1994; Hardegree and Van Vactor 1999; Leblanc et al. 2003; Larsen and Bibby 2005; Hardegree 2006; Qiu et al. 2006). No similar studies have been conducted on conifers. Base temperature and thermal time requirements are parameters in the thermal time model that can be used to study variation in germination. Determining the thermal time requirements for jack pine, white spruce, and black spruce will allow prediction of seed germination under current and future climates. These species may have spatial variation in dormancy characteristics and germination requirements, reflecting adaptations to local climatic conditions such as temperature and precipitation. Thermal time models are useful because model parameters are physiologically significant and can be used for comparing different seed lots (Covell et al. 1986; Ellis et al. 1986; Hardegree 2006). These parameters may also be related to environmental variables and can then be linked to climate change models to determine the impacts of increased temperature on the conifers, as well as to determine which ecotypes are best adapted for regeneration. Natural selection may favor species that match germination with the

most suitable times for plant growth (Jurado and Flores 2005). Therefore, germination patterns along environmental gradients such as longitude, latitude, precipitation, and temperature are expected, which can in turn be used to predict regeneration under climate change scenarios. A temporal shift in the germination of these conifers to an earlier time in the season is expected with increasing temperatures. Southern locations in the boreal forest will be the most affected because it is the most at risk to elimination under climate change (Hogg and Hurdle 1995).

The objectives of this study were to: 1) determine the dormancy and germination of white spruce, black spruce and jack pine seeds from geographically distinct ecoregions within the Boreal Plain Ecozone of Saskatchewan; 2) use the thermal time model to determine differences in the base temperature and thermal time requirements for germination among collections; 3) determine if parameters for thermal time models can be linked to environmental gradients; 4) predict potential impacts of climatic change on the regeneration of these species in the Mixed Wood Forest of Saskatchewan, and; 5) identify collections that may persist under future climatic conditions. It was hypothesized that the requirements for dormancy breaking and germination vary among species and collections, and base temperatures and thermal time requirements vary with latitude, longitude, temperature, and precipitation. The hypothesis that the future temperature as predicted by Canadian Global Climate Model will favor earlier germination in spring, and collections with higher base temperatures will have improved germination under warmer temperatures and therefore, represent species that will perform better under climate change was also tested.

2.0 LITERATURE REVIEW

2.1 Ecoregions of the Mixed Wood Forest of Saskatchewan

Wiken (1986) defined ecoregions as a form of ecological land classification, which is:

> a process of delineating and classifying ecologically distinctive areas of the Earth's surface. Each area can be viewed as a discrete system, which has resulted from the mesh and interplay of the geologic, landform, soil, vegetative, climatic, wildlife, water, and human factors that may be present. The dominance of any one or a number of these factors varies with the given ecological land unit. The holistic approach to land classification can be applied incrementally on a scale-related basis from site-specific ecosystems to very broad ecosystems.

This system provides a standard framework within which we can expand and integrate our knowledge of the land, including plants and animals, the prevailing ecological processes, as well as human impacts related to the development and the conservation of land resources (Fung 1999). Three levels in this classification system are Ecozone, Ecoregion, and Ecodistrict/Landscape Areas (http://sis.agr.gc.ca/cansis/nsdb/ecostrat/intro.html). Ecozones define the ecological mosaic of Canada on a sub-continental scale, and divide Canada into 15 terrestrial ecozones. They differentiate an area of the earth's surface representative of large and very generalized ecological units characterized by interactive and adjusting abiotic and biotic factors. Ecoregions are a subdivision characterized by distinctive regional ecological factors, including climate, physiography, vegetation, soil, water, and fauna. Ecodistricts are a subdivision of an Ecoregion characterized by distinctive assemblages of relief, landforms, geology, soil, vegetation, water bodies, and fauna (http://sis.agr.gc.ca/cansis/nsdb/ecostrat/intro.html).

Saskatchewan consists of four Ecozones, 11 Ecodistricts and 157 landscape areas (Fung 1999). The four Ecozones in Saskatchewan are the Taiga Shield, Boreal Shield, Boreal Plain, and Prairie. The Boreal Plain is the focal point for this study because all seeds of three species were collected from this Ecozone. The Boreal Plain forms a wide band across the middle of Saskatchewan, covering just over a quarter of its landmass. Here the northern reaches of agriculture and the beginning of the boreal forest merge; this Ecozone is dominated by coniferous trees such as pine (*Pinus*), spruce (*Picea*) and tamarack (*Larix laricina* (Du Roi) K.Koch) (http://www.parklandpublishing.com/secrets/introduction.htm). Within this Ecozone are three distinct Ecoregions, the Mid-Boreal Upland, Mid-Boreal Lowland, and the Boreal Transition. Each of these regions is divided into several landscape areas.

2.1.1 Mid-Boreal Upland

This Mid-Boreal Upland Ecoregion is approximately 10,150,000 ha in size, or 16% of Saskatchewan's total land area (Fung 1999). The climate is sub-humid and cool, marked by short, cool summers and long, cold winters and considered a subarctic climate (http://interactive.usask.ca/ski/environment/ecoregions). It is characterized by an ascending sequence of steeply sloping, eroded escarpments, hilly glacial till plains, and level plateau-like tops (Fung 1999). This region consists of loamy, gray soils that produce taller trees than in the Churchill River Upland where soils become sandy and poorly drained (http://www.virtualsk.com/maps/ecoregions_5.html). Aspen (*Populus tremuloides* Michx), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (P. Mill) B.S.P) and tamarack are common in this Ecoregion, and account for the bulk of the province's merchantable timber (Fung 1999). White spruce grows where moisture conditions are favorable. Jack pine dominates sandy areas and is mixed with black spruce on the

plateau-like tops of the uplands, while black spruce flourishes in low-lying peatland areas (Fung 1999).

2.1.2 Mid-Boreal Lowland

The Mid-Boreal Lowland Ecoregion is smaller than the Mid-Boreal Upland consisting of 2,354,000 ha, or 3% of Saskatchewan's total land area (Fung 1999). The climate is subhumid, cold and subjected to late spring and late fall frosts. Summers are short and cool, and winters are long and cold (http://interactive.usask.ca/ski/environment/ecoregions). It is a relatively flat, low-lying Ecoregion dominated by wetlands. The northern part of this region supports peatlands with open stands of tamarack and black spruce. To the south lies the floodplain of the Saskatchewan River and associated levees, marshes, fens and poorly drained meadows (Fung 1999). Balsam poplar (*Populus balsamifera* L.), white spruce, aspen and some associated hardwoods are common within the southern area.

2.1.3 Boreal Transition

The boreal transition makes up 5,403,000 ha, 8% of Saskatchewan's total land area (Fung 1999). The climate is subhumid and cool, encouraging the production of forage crops (http://interactive.usask.ca/ski/environment/ecoregions). This mix of forest and farmland marks the southern advance of the boreal forest and encompasses the northern limit of arable agriculture (Fung 1999). Gray soils support white spruce and jack pine throughout the area, but they are less common than in the more northern Ecoregions. Peatlands are also infrequent within this region.

2.2 Ecology of white spruce, black spruce and jack pine

2.2.1 White spruce

White spruce is within the family Pinaceae. It has a transcontinental range, from Newfoundland and Labrador to the west across Canada along the northern limit of trees to Hudson Bay, Northwest Territories, and Yukon (http://na.fs.fed.us). Generally it increases in importance from east to west (McLeod and MacDonald 1997), and it is a "plastic" species because of its ability to grow under highly variable conditions, including extreme climates and soils (http://na.fs.fed.us). White spruce grows in climatic conditions ranging from eastern Canada's wet maritime regions to semi-arid conditions in the continental west (Nienstaedt and Zasada 1990). This species grows in soil materials that range from peat and sand, to clay of glacial, lacustrine, marine, fluvial or aeolian origin (Zoltai 1975). Podzolic soils predominate over the range of the species, but white spruce also grows in brunisolic, luvisolic, gleysolic, and regosolic soils (http://na.fs.fed.us). In Saskatchewan, white spruce grows best on moderately well-drained clay loams (Kabzems 1971). White spruce is able to grow on extremely diverse sites, from acidic to alkaline soils and acidity (pH) values from 4.7 to 7.0 (Ph 4.7-7.0) (http://na.fs.fed.us). White spruce is less tolerant than black spruce of highly acidic soils (Ritchie 1987), and has greater nutrient requirements than others in its family (Nienstaedt and Zasada 1990). It can reach 250-350 years of age and outlive jack pine and black spruce (Richie 1987). White spruce, a long-lived climax species, co-dominates or forms a significant part of the vegetation in mixed stands with balsam fir (*Abies balsamea* (L.) P. Mill) and black spruce. White spruce gradually replaces pine, aspen, birch (*Betula papyrifera* Marsh.), and/or poplar on well-drained sites. It grows less frequently as an early successional species, but can form pure stands or mix with hardwoods immediately after fire

(http://www.rook.org/earl/bwca/nature/trees/piceaglauca. html). This tree may be suppressed by more rapid and early growth of other trees and remains an understorey species for upwards of 50-70 years (McLeod and MacDonald 1997). This species is monoecious and reaches reproductive maturity around 30 years of age, with peak seed production at approximately 60 years (McLeod and MacDonald 1997). Although 4-year-old trees can produce cones and seeds, production is usually low (Sutton 1969). Vegetative reproduction by layering is rare, but does occur in northern regions where layering is important in maintaining populations (Richie 1987).

2.2.2 Black spruce

This species ranges from northern Massachusetts to northern Labrador on the Atlantic coast, west across Canada to the west coast of Alaska. The southern limits of black spruce consist of isolated patches in the northern part of the United States and west across south-central Saskatchewan, Alberta, and central British Columbia. This tree has a wide distribution within the boreal forest, is immensely important as a tree line species (Black and Bliss 1980), and forms the latitudinal tree line in northeastern and north-central Canada (McLeod and MacDonald 1997). Climate across the range of this species varies from dry continental in the northwest to the wet maritime conditions of Newfoundland (Richie 1987). Black spruce is restricted to very wet, peaty sites (Black and Bliss 1980) and tolerates cold permafrost soils (Richie 1987). In the south, black spruce is often limited to peat bogs, tolerating acidic soil conditions, but it grows on a range of soil types in the central and northern parts of its range (Ritchie 1987). Soils where black spruce grows can vary from deep humus, to clays, loams, sands, coarse till, boulder pavements, and shallow soil mantles over bedrock. The most productive black spruce stands are on dark brown to blackish peats, which usually have a considerable amount of decayed woody materials. Stands of low productivity are usually found on thick deposits of partially decomposed

sphagnum peat (http://www.rook.org/earl/bwca/nature/trees/piceamar.html). Depending on the soil substrate, black spruce can grow in association with balsam fir (*Abies balsamea* (L.) P. Mill.), paper birch (*Betula papyrifera* Marsh.), tamarack, white spruce and aspen on clay or loamy soils. On organic sites, black spruce can grow in mixed stands containing tamarack, western white pine (*Pinus monticola* Dougl. ex D. Don), and balsam fir. Black spruce is associated with Schreber's big red stem moss (*Pleurozium schreberi* (Brid.) Mitt.), splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp. in B.S.G.), knights plume moss (*Ptilium crista-castrensis* (Hedw.) De Not.), sphagnum moss (*Sphagnum* spp.), sedges (*Carex* spp.) and speckled alder (*Alnus incana* (L.) Moench ssp. Rugosa (Du Roi) Clausen) in climax communities (http://www.rook.org/earl/bwca/nature/trees/piceamar.html). Black spruce commonly reaches ages between 100 and 200 years (McLeod and MacDonald 1997) and the production of seeds can start at 10 years of age, but the quantity is not large; trees older than 30 years often hold large amounts of seeds but yields diminish as the cones age (Skeates et al. 1989). Black spruce is a semi-serotinous species. Cones release some seeds in autumn, but the majority is released over several years (Hosie 1979; Haavisto 1987; Viereck and Johnston 1990; McLeod and MacDonald 1997). High temperatures caused by fire encourage cone opening and seed release (McLeod and MacDonald 1997), allowing rapid seedling establishment. Seeds are usually not destroyed by fire because cones are located in the upper part of the crown where they are least likely to burn (http://www.rook.org/earl/bwca/nature/trees/piceamar.html). Therefore, this species is considered moderately fire dependant and a post-fire pioneer (McLeod and MacDonald 1997).

2.2.3 Jack pine

The majority of the jack pine is distributed within Canada, where its northern boundary extends eastward from the Mackenzie River in the Northwest Territories across the country to Cape Breton Island, Nova Scotia (http://na.fs.fed.us). The range extends southwest through Maine, New Hampshire, northern New York, central Quebec and northern Ontario, Michigan, extreme northwest Indiana, northeast Illinois, then northwest through Wisconsin, Minnesota, Manitoba, Saskatchewan, central Alberta, to extreme northeast British Columbia. Its northwest limit may be set by growing season length and mean annual degree-days, while in the northeast it appears to be limited by its intolerance of deep snow. Southern limits are influenced by soil moisture; additional stress forms the eastern boundary and summer temperatures restrict it in the west (McLeod and MacDonald 1997). The climatic range for this species varies from maritime in the east, to diverse continental climates characterized by short, warm to cool summers, very cold winters, and low rainfall in the west (http://na.fs.fed.us).

Jack pine usually grows on level to rolling topography, on light sandy or gravelly soils with very good drainage and aeration (McLeod and MacDonald 1997), but the tree also grows on loamy soils, over limestone, on peat, over permafrost, on thin soils over granites, and metamorphosed rocks of the Canadian Shield (http://na.fs.fed.us). It grows best on well-drained, loamy sand where the midsummer water table is 1.2 to 1.8 m below the surface (http://na.fs.fed.us). This tree is usually out-competed on those sites and becomes restricted to nutrient-poor and rocky upland sites and outcrops with thin soils (McLeod and MacDonald 1997).

During the first 20 years of establishment, jack pine is the fastest growing conifer other than tamarack (Rudolf 1965). Stands begin to disintegrate after 80 years on the best sites, and

after 60 years on the poorest sites, however a 230-year-old tree was discovered in Ontario (http://na.fs.fed.us).

Jack pine is monoecious, and produces serotinous cones over the majority of its range, although in the southern part of its range cones are non-serotinous (Rudolf 1965). Seeds are released when temperatures reach at least 27ºC or when high temperatures produced by fires melt the resinous scale-bonding materials (Rudolph and Laidly 1990). Cones are produced at an early age, sometimes in their fourth or fifth year, and seeds can remain viable within them for 20 years or more (Henry 2002). Jack pine is considered fire dependent, and dominates in areas with a high fire frequency. Along with promoting seed release, fire prepares a suitable seedbed by combustion of the organic layer (Rudolph and Laidly 1990). Common tree species associated with jack pine include: balsam fir, red maple (*Acer rubrum* L.), tamarack, white spruce, balsam poplar, bigtooth aspen (*Populus grandidentata* Michx.), quaking aspen (*Populus tremuloides* Michx.), bur oak (*Quercus macrocarpa* Michx.), and northern red Oak (*Quercus rubra* L.) (http://www.rook.org/earl/bwca/nature/trees/pinusbank.html).

2.3 Seed dormancy and germination

Dormancy is a naturally occurring phenomenon of many plants to maximize the chances of seedling establishment (http://www.passionflow.co.uk/downloads/seed%20dormancy201997.pdf), and is considered a mechanism for optimizing the distribution of germination in time or space (Bewley and Black 1982). Simpson (1990) defined dormancy as a "temporary failure of a viable seed to germinate, after a specified length of time, in a particular set of environmental conditions that later evoke germination when the restrictive state has been terminated by either natural or artificial means". Simpson's statement implies that dormancy should not be a measure of the external conditions a seed is currently exposed to, but be a characteristic of the seed

(Vleeshouwers et al. 1995). Vleeshouwers et al. (1995) proposed that dormancy is a seed characteristic, the degree of which defines what conditions should be met to allow the seed germinate, and the wider the range of conditions at which a seed is able to germinate, the smaller its degree of dormancy.

Depending upon the type of dormancy, stratification, light, leaching, scarification, growth regulators, dry storage/elevated temperatures, exposure to chemicals, fluctuating temperature conditions, or high O_2 concentrations may break dormancy and promote germination (Bradbeer 1988). Once seeds have survived various hazards that accompany their ripening, dispersal, and dormancy phases, they are ready for germination to begin provided the proper environmental cues are encountered. It is rare for North American forest trees to have seeds in which germination follows simply from exposure to moisture, good aeration, and appropriate temperature; exceptions are poplar, willow (*Salix*) and one species of maple (*Acer*) (Farmer 1997). Usually preconditioning or special conditions, such as stratification, are required to release dormancy and initiate germination of seeds for species from the boreal forest.

2.3.1 Types of dormancy

Dormancy can be classified as primary (innate) dormancy or secondary (induced) dormancy. Primary dormancy is the establishment of dormancy during seed development and maturation (Bewley and Black 1994). Secondary dormancy is induced in mature seeds, which subsequently lose their ability to germinate readily (Mayer and Poljakoff-Mayber, 1982). Nikolaea (1977) divides dormancy types into those that are "endogenous" due to properties of the embryo and those that are "exogenous" casued by properties of the endosperm or any other tissues of the seed or fruit.

Physical dormancy is exogenous, meaning the seed coat prevents entrance of water and/or oxygen to the embryo, contains chemical inhibitors, physically restricts growth of the embryo, or modifies the light reaching the embryo (Bewley and Black 1982; Farmer 1997). The seed coat includes the pericarp, testa, perisperm, and endosperm, all enclosing the embryo (Bradbeer 1988). Embryos of seeds in a state of physical dormancy are usually capable of normal growth, but do not germinate because its life processes cannot be activated (Nikolaeva 1969). Physical dormancy of the embryo has been shown in species such as maple that are particularly well known for their rapid germination when seed coats are removed (Farmer 1997). Complete removal of the seed coat is not always necessary; physical, mechanical, or chemical treatments can often allow embryo germination (Nikolaeva 1969; Bewley and Black 1982). Embryo dormancy occurs when the control of dormancy resides within the embryo itself. The control of embryo dormancy may involve cotyledons, germination inhibitors, or an immature embryo (Bewley and Black 1982). Evidence suggests that cotyledons are responsible for inhibiting the growth of the axis in dormant embryos. For example, in European euonymus (*Euonymus europaeus* L.), dormancy is broken by cutting off one cotyledon (Bewley and Black 1982). Many substances can inhibit germination, such as courmarin, auxins, gibberellin, and phenolic compounds of various kinds (Mayer and Poljackoff-Mayber 1982). Embryos of several species are morphologically immature when the dispersal unit is released, and require a period of further development before they can germinate. Immature embryos are characteristically small, and may be poorly differentiated (Bewley and Black 1994). The time required for the completion of embryo development determines the depth of dormancy of these seeds (Nikolaeva 1969).

2.3.2 Dormancy release by temperature and light

Many factors release seeds from dormancy, including light, low or high temperatures, alternating temperatures, water, fire, aging, and changes in the covering structures (for details see Bryant 1985; Bewley and Black 1994). The effectiveness of these factors is species specific (Fenner 1985). Only light and temperature will be discussed here because their relevance to this study.

Temperature is the main factor governing changes in seed dormancy (Bouwmeester 1990). As in summer annuals like prostrate knotweed (*Polygonum aviculare* L.), low winter temperatures alleviate dormancy (Kruck and Benech-Arnold 1998), allowing seeds to germinate in the spring under favorable conditions. Alternatively, high summer temperatures reinforce dormancy (Karssen 1982; Batlla et al. 2003) and prevent seeds from germinating in the fall. This process is reversed in winter annuals. Perennials can have three types of dormancy, exogenous, endogenous and a combination of the two types. In exogenous dormancy, high temperatures caused by fire can often break physical dormancy. In endogenous dormancy, morphological dormancy can be overcome by alternating warm and cool temperatures or by stratification depending on species, while some tropical species require high temperatures to break this type of dormancy (http://trc.ucdavis.edu/egsutter/plb171/lecturespdf4/5-Seed%20dormancy02.pdf).

Chilling or stratification can break seed dormancy in most non-tropical species, especially in conifers. Dormancy can be released when hydrated seeds experience relatively low temperatures, generally in the range of 1-10ºC, but in some cases as high as 15ºC (Bewley and Black 1994). Chilling conifer seeds before germination usually increase the rate of germination and more complete germination over a wide range of temperatures (Farmer 1997). A stratification requirement prevents seeds from germinating in the fall even if the environment is otherwise suitable for germination (Fowler and Dwight 1964).

Chilling can break dormancy in species with embryo, coat imposed, primary, conditional, or secondary dormancy (Bewley and Black 1994). The rapidity with which this germination capability develops varies with species and with individual seeds within species (Farmer 1997). For example, many woody species require a prolonged stratification (e.g., up to 180 days for downy hawthorn (*Crataegus mollis* Scheele.)) while, some herbaceous species need just a few days of stratification (e.g., only 12 hours in wheat (*Triticum*)) (Bewley and Black 1994).

Constant chilling temperatures may not be enough to break dormancy in some species. Many species require temperature fluctuations for dormancy breaking because seeds are commonly subject to low night temperature and high daytime temperatures in the field. In threelobe beggarticks (*Bidens tripartitus* L.), cultivated tobacco (*Nicotiana tabacum* L.), and dock (*Rumex* L.), dormancy can only be broken with fluctuating temperatures, with the maximum effect at the greatest temperature differences (Bewley and Black 1994).

Light is important for releasing seeds from dormancy (Bewley and Black 1994). Almost all light-requiring seeds have coat-imposed dormancy, and the only types of conifer seeds that respond to light have conditional dormancy (Bewley and Black 1994; Farmer 1997). When imbibed seeds of certain species are exposed to natural or artificial light containing wavelengths from 500-800 nm, they exhibit greater germination at a given temperature (Farmer 1997). This phenomenon occurs in some species of pine and birch (Farmer 1997). Other species are affected by exposure to white light that can range from just a few minutes in lettuce (*Lactuca* L.) to an hour in some pine and birch species, or by intermittent exposure as in Madagascar widow's-trill (*Kalanchoe blossfeldiana* Poelln.) (Bewley and Black 1994; Farmer 1997). Often the effect of light depends on the temperature, as the promotive effect of light is frequently greater at higher

temperatures, and chilling after imbibition almost always favors complete germination in darkness (Fraser 1971).

Phytochrome is involved in most of the dormancy breaking by light (Borthwick et al. 1952; Farmer 1997). Red light (640-680 nm) stimulates germination by converting phytochrome from an inactive (P*r*) form to an active (P*fr*) form. Darkness causes a reversion of P*fr* to P*r,* and it is believed that the radicle is the light sensitive part of the embryo (Farmer 1997). Seeds in natural conditions have a shifting P*r* – P*fr* balance depending upon light quality and photoperiod. Seeds germinate when the balance shifts toward more P*fr*. The balance required for germination varies among species and probably among individual seeds within species, which accounts for differences in light response (Farmer 1997).

2.3.3 Stages in germination

Germination includes all the processes involved in the transformation of a plant embryo into an independent, established seedling (Bryant 1985). Three stages of germination include 1) imbibition of water, 2) mobilization and use of food reserves such as carbohydrates, fats and proteins, and 3) growth (Farmer 1997). Conditions required for germination include an adequate supply of water, a suitable temperature and oxygen (Mayer and Poljakoff-Maber 1982)

The following equation is given by Farmer (1997) to describe seed water uptake during imbibition:

$$\Psi w = \Psi \pi + \Psi m + \Psi p \qquad (2.1)$$

where Ψw is the total water potential of a seed, $\Psi \pi$ is the osmotic potential, Ψm is the matric potential, and Ψp is hydrostatic pressure which exists because cells have relatively rigid walls (Farmer 1997). The water potential of a dry seed is usually negative enough to cause water to

move from a moist environment into the seed; this process is imbibition, the first stage of germination. Under favorable moisture and temperature conditions, physical water uptake takes about 8 hours in conifer seeds (Farmer 1997). The extent to which imbibition occurs is determined by the composition of the seed, the permeability of the seed coat to water, and the availability of water in liquid or gaseous form in the environment (Mayer and Poljakoff-Mayber 1982). All seeds require sufficient moisture for imbibition and germination; most seeds will even germinate with an excess of water. In some cases excessive water will reduce the permeability of the seed coat to oxygen and inhibit germination as shown in common beat (*Beta vulgaris* L.) and spinach (*Spinacea oleracea* L.) (Gulliver and Heydecker 1973; Bradbeer 1988). In natural conditions, seeds often face environments in which water potentials fluctuate from 0 to -2.0 MPa. Most conifer seeds can withstand the stress associated with this wetting and drying, and are described as orthodox seeds (Farmer 1997).

After imbibition, respiration increases and provides energy in the form of ATP needed to drive other processes, and existing sugars are used as the initial substrates for respiration. This reaction is instigated by the uptake of water in the seed, which hydrates proteins and causes many complex chemical changes. Three types of changes occur within this time including 1) the breakdown of materials, 2) transport of these from one area of the seed to another, and 3) production of new materials from the breakdown products (Mayer and Poljakoff-Mayber 1982). The seed takes up only water and oxygen at this phase of germination. When the radicle emerges from the seed and growth begins, respiration and adenylate levels increase dramatically (Farmer 1997). Once the seedling has formed and a root is present, minerals can be taken from the soil and the cotyledons exposed to light can begin photosynthesis (Mayer and Poljakoff-Mayber 1982).

2.4 Dormancy characteristics and germination requirements for the three selected conifers

2.4.1 White spruce

The testa is principally responsible for imposing dormancy in white spruce seeds, although the magagametophyte and/or nucellus also play a role (Downie and Bewley 1996). During moist chilling, these tissues undergo significant weakening which allows the seed to germinate. Therefore, they concluded that the white spruce embryos do not exhibit innate dormancy. Alleviation of seed dormancy in white spruce is dependent on the degree of seed hydration (Downie et al. 1998). Moist chilling did not alleviate dormancy at or below 20% Moisture Content Fresh Weight (MCFW). When seeds were moist-chilled at 25% more water content, maximum germination occurred after one week. If seeds were non-dormant, there was no significant difference in percentage of germination at any moisture content between10 and 40%. Germination decreased after seeds were moist-chilled for four to five weeks.

White spruce has a maximum germination temperature between 29ºC and 35ºC, a minimum temperature of 5ºC, and germination usually stops below 10ºC (http://na.fs.fed.us). Under natural conditions, white spruce seeds remain viable for 1 to 2 years. Seeds can overwinter under snow and germinate in the spring or summer when water is sufficient and soil temperature is favorable, reaching 50-70% final germination (http://na.fs.fed.us). White spruce is often classified as having conditional dormancy that varies in response to temperature and light. Under light and warm temperatures, white spruce can reach 70% germination with no stratification (Safford 1974).

2.4.2 Black spruce

Black spruce and white spruce have similar patterns of conditional dormancy (Farmer 1997). Black spruce has a mild dormancy, that allows substantial germination in darkness of unchilled seed at high temperatures and complete germination over a range of temperatures

under long photoperiods (14+hr). After a short period of chilling (<30 days), seeds can germinate rapidly over a wider temperature range under dark conditions (Farmer 1997).

Few data were available describing the germination requirements of this species. Farmer (1997), however, stated that for most tree species, germination occurs slowly at 1-5ºC. Temperatures from 35-45ºC limit germination and the optimal temperature is usually around 20-25ºC.

2.4.3 Jack pine

Pines with serotinous cones such as jack pine can complete germination rapidly once dispersed after fire. Cone serotiny suggests no dormancy or a mild conditional dormancy is present (Farmer 1997). Jack pine does not respond to chilling when subsequently incubated at high temperatures (20-30ºC). Germination is promoted in jack pine seeds when they are exposed to a short (<10 min) period of red light followed by dark incubation at 16ºC; however, this effect does not occur at 21ºC (Ackerman and Farrar 1965; Farmer 1997). Light can also promote germination by daily exposures longer than 8 hours (Ackerman and Farrar 1965). Therefore, jack pine seed displays conditional dormancy that can be broken by long exposure to light or by a short burst of red light under low temperatures, a condition not commonly found in other woody species (Farmer 1997). Light does not effectively "trigger" germination until the threshold moisture content is reached in the seed, which is around 30 minutes of imbibition in jack pine (Ackerman and Farrar 1965). Optimal conditions for jack pine seeds to germinate are adequate moisture, light, and temperatures ranging from 16-27ºC. Germination is reduced at all temperatures when light is excluded. Jack pine seeds usually germinate within 15 to 60 days under favorable conditions (Rudolph and Yeatman 1982).

2.5 Ecotypes and spatial variation in germination

Turesson (1922) coined the term ecotype, describing it as 'groupings of populations (ecological races, subspecies) in relation to a type of habitat or climate' (Quinn 1978). The term is now used by ecologists to indicate almost any degree of variation below the level of species that is genetically based and correlated with habitat (Quinn 1978). Ecotypes are perceived as genotypic responses and adaptations to particular habitats (McKell et al. 1962).

Most forest tree species show genetic variation at the regional scale, in response to variation in environmental conditions (Morgenstern 1996). Identifying individual seed sources or populations may allow indirect estimates of the potential response of an individual species to climate change (Andalo et al. 2005). These populations may also be of aid when identifying potential seed sources for maintaining current forest stands in the face of climate change or for colonizing new stands (Hufford and Mazer 2003). The existence of ecotypes in coniferous tree species has been studied extensively. Many different ecotypes have been identified, such as photoperiodic, climatic, edaphic, altitudinal, latitudinal, and biotic ecotypes (Hiesey et al. 1942; Fowler and Dwight 1964; Vaartaja 1959; Quinn 1978). Vaartaja's (1959) work on photoperiodic ecotypes in trees concluded that because climatic factors change gradually from one location to another, there might also be a gradual change between ecotypes due to neighboring trees exchanging genes. To properly study ecotypic variation, seeds should be selected from geographically distant sources (Vaartaja 1959; Quinn 1978). Comparisons between very distant sources yield clearer evidence of the range of ecotypic variation because the interactions are large and more obvious (Vaartaja 1959).

Many studies have examined ecotypic differentiation in seeds (Habeck 1958; Mergen 1963; Fowler and Dwight 1964; Wang et al. 1994). Seeds are usually collected from populations over a wide range of altitudes and/or latitudes, and their dormancy and germination characteristic

are compared (Baskin and Baskin 1973). For example, genetic differences among eight seed sources were illustrated for eastern white pine (*Pinus stobus* L.) (Mergen 1963). Seeds from northern sources germinated faster, and dormancy was broken by a shorter period of stratification than southern sources (Mergen 1963; Fowler and Dwight 1964). Stratified seeds of white cedar (*Thuja occidentalis* L.) from upland sites had a greater germination (85.3%) than those from bottomland sites (72.8 %) (Habeck 1958). Germination of unstratified seeds from the two sites was not different (77.3% and 76.8% respectively). Baskin and Baskin (1973) argued that the environment of seeds during maturation may cause differences between populations, and seeds are not necessarily genetically different. Sufficient evidence is available to show that environmental conditions during maturation can significantly affect dormancy and germination characteristics of seeds.

2.5.1 White spruce ecotypes

White spruce seeds exhibit variable percentage of germination depending on seed origin. For example, white spruce seeds from central Ontario do not germinate under any condition unless chilled for two weeks. Unchilled Alaskan white spruce had 90% germination under a 22 hr photoperiod at moderate temperatures (Farmer 1997). Caron et al. (1990) showed the degree of primary dormancy could vary among cones on the same tree in white spruce. Cardinal temperatures (base, optimum, and maximum) for germination of seeds after 28 days were determined for six provenances of white spruce across varying latitudes (Fraser 1971). Optimal temperatures varied from 12.7ºC to 23.9ºC among seeds originating from British Columbia, Ontario, New Brunswick, and New York, but no relationship between germination response and latitude, elevation, or precipitation was found. Seeds obtained from cooler, northerly sources had matching cardinal temperatures, similar responses to temperature, and germinated faster at a lower temperature than other provenances studied (Fraser 1971). These responses support the

theory of environmental preconditioning suggested by Rowe (1964), which states that germination response to temperature is influenced or conditioned by the environment in which the seed originated (Fraser 1971). A significant proportion of the total phenotypic variation in white spruce growth could be explained by the geographic origin of seeds (Andalo et al. 2005). This study investigated the effects of temperature and precipitation on 45 distinct geographical seed sources across Ontario and Quebec. Temperature was the most important factor causing differentiation in white spruce populations, suggesting that white spruce growth is locally adapted to the temperature (Andalo et al. 2005). White spruce seed also has strong north-south trends in seed weight, germinative capacity, hypocotyl length, cotyledon numbers, and seedling height; east-west trends in seed weight, cotyledon numbers, and seedling height (Khalil 1986). Germination capacity and juvenile characteristics were positively correlated with seed weight which in turn varied among provenances (Khalil 1986). Provenance differences can also affect the phenology, growth and wood density of white spruce (Nienstaedt and Teich 1972; Corriveau et al. 1987; Li et al. 1993; Lesser and Parker 2004). Frost tolerance in white spruce during the early seedling stage, varied with the provenance of seed origin, but variation was inconsistent from one developmental stage to another (Coursolle et al. 1998). This variation indicates each provenance has specific and different photoperiods and/or temperatures that trigger the onset of hardening, thus reflecting their ability to adapt to the environmental conditions of local habitats (Coursolle et al. 1998).

2.5.2 Black spruce ecotypes

Genetic variation in black spruce is clinal, primarily along a north-south geographical gradient (http://na.fs.fed.us). Differences in productivity, survival rate, and response to photoperiod have been linked to the geographical area of seed origin. Clinal variation in black spruce in the Maritime Provinces caused three overlapping breeding zones (Park and Fowler

1988). Within the range of black spruce, extensive gene flow between stands discourages the formation of distinctive provenances. Phenotypic characteristics of cones, needles, twigs, percentage survival, and growth generally differ more within-populations than between-populations (Fowler and Mullin 1977; Parker et al. 1983; Thomson et al. 1990). In Alberta, black spruce populations growing on strongly contrasting environments, such as uplands adjacent to peatlands, exhibited similarity in isozyme variability (Wang and MacDonald 1991). In contrast, populations near the margins of the range, such as coastal regions in Newfoundland, better reflected provenance effects (Khalil 1984; Yeh et al. 1986; http://na.fs.fed.us).

2.5.3 Jack pine ecotypes

In species with a nearly transcontinental distribution such as jack pine, the variation between different provenances is likely to be considerable. Large differences in size and form of the jack pine trees were evident with northern provenances showing slower growth than southern ones (Giertych and Farrar 1962). The height and growth of two-year old seedlings also correlated positively with the number of degree-days of the locality of origin and inversely correlated with latitude (Stoeckeler and Rudolf 1956). Height, dry weights of foliage and roots, and dry weight of seeds for different jack pine provenances also correlated with growing degree-days (Giertych and Farrar 1962).

2.6 Using thermal time models to study seed germination

Temperature (T) has a primary influence on seed dormancy and germination, affecting both the capacity for germination by regulating dormancy and the rate or speed of germination in non-dormant seeds (Alvardo and Bradford 2002). Three cardinal temperatures (maximum, minimum and optimum) describe the range of T over which seeds of a particular species can germinate (Bewley and Black 1994). The minimum or base temperature (T_b) is the lowest T at which germination can occur, the optimum temperature (T_o) is the T at which germination is

most rapid, and the maximum or ceiling temperature (T_m) is the highest T at which seeds can germinate. The temperature for germination is sensitive to the dormancy status of seeds, often being narrow in dormant seeds and widening as dormancy is lost (Vegis 1964).

Many mathematical models have been developed to describe germination patterns in response to T (e.g, Garcia-Huidobro et al. 1982; Ellis and Butcher 1988; Leblanc et al. 2003). For suboptimal temperatures (from T_b to T_o), germination timing can be described on the basis of thermal time or heat units (Alvarado and Bradford 2002). Thermal time ($\theta_{T(g)}$), the T in excess of Tb multiplied by the time to a given germination percentage (tg), is a constant for that percentage (the thermal time constant, $\theta_{T(g)}$):

$$\theta_{T(g)} = (T - T_b)t_g \tag{2.2}$$

$$GR_{(g)} = 1/tg = (T - T_b)\, tg/\, \theta_{T(g)} \tag{2.3}$$

(Alvarado and Bradford 2002)

The germination rate for a given seed fraction or percentage g ($GR_{(g)}$, or $1/t_{(g)}$) is assumed to have a linear function with T above T_b, a slope of $1/\theta_{T(g)}$ and an intercept on the T axis of T_b. Thermal time models (Eqns 2.2 & 2.3) have been extensively and successfully applied to describe seed germination timing at suboptimal temperatures (Alvarado and Bradford 2002). Seed treatments such as stratification modify the physiological status of seeds and affect germination percentage, germination rate and/or seedling vigor (Wang 2003).

A probit cardinal temperature model can be used as a population-based method to analyze germination time courses at different sub-optimal temperatures to estimate T_b (Hardegree 2006). This method combines complete original germination time course data in a

single regression to determine the base temperature and also provides an estimate for the variation in $\theta_{T(g)}$ among seeds (Hardegree 2006). The probit cardinal temperature model can be described by the following formula if the variation of $\theta_{T(g)}$ within a seed population follows a normal distribution:

$$\text{Probit}(g) = \frac{(T-Tb)*t(g) - \theta T(50)}{\sigma_{\theta T}} \qquad (2.4)$$

(Dahal et al. 1990)

The advantages of this model include its efficiency at comparing seedlots for relative temperature responses, predicting germination rate and time. Parameters can be related to underlying physiological processes that determine cumulative temperature response and it has proven accurate in predicting germination rate and time (Hardegree 2006)

2.7 Climate change and its potential impact on the Mixedwood forest of Saskatchewan

Global warming, due to increased concentrations of atmospheric CO_2 and other greenhouse gases, is expected to be amplified in middle and higher latitudes across the earth, including the tundra and boreal biomes of North America, Europe and Asia (Rizzo and Wiken 1992; Price et al. 1999). Consequently, ecosystems in these latitudes will experience more pronounced climatic variation (Rizzo and Wiken 1992) triggering major changes in the earth's living systems (Iverson and Prasad 1998). The majority of recent General Circulation Models (GCMs) predicts relatively large changes in the climate of the western Canadian interior as a consequence of increases in the concentrations of atmospheric CO_2 and other greenhouse gases (Hogg and Hurdle 1995). Many studies have been devoted to predicting these potential changes in the earth's biota, especially with respect to the potential necessary migration of plant species (Iverson and Prasad 1998). In Canadian ecosystems, ecological shifts will most likely arise, however, a considerable lag may occur before vegetation and soils reflect a new prevailing

climate (Rizzo and Wiken 1992). Vegetation zones are not entirely determined by shifts in climate; soil, local topography, groundwater level, and other factors may influence plant species distributions (Talkkari and Hypen 1996). Different tree species or populations may also have different response potentials to climate change through plasticity, genetic adaptation (Rehfeldt et al. 1999) and the capability to migrate through complex landscapes (Schwartz et al. 2001).

Climatic warming has occurred throughout the history of the earth. During the Holocene period climate warming was at a lower rate that is currently projected by GCMs, but many important inferences concerning species migration can be derived from that period of time. Past history has shown that: 1) species did shift their geographical ranges, generally northward because of warming; 2) species' responses were individualistic (Iverson and Prasad 1998). Under current climatic change scenarios and fragmented landscapes, many species may have difficulties in expanding their range during rapid climate change (Iverson and Prasad 1998). Future dynamics of the boreal forest is further complicated by tree life cycles taking several decades to complete, and their rate of dispersal, invasion and ability to form closed forests in areas which become climatically suitable is much slower relative to most non-arboreal species (Solomon and Kirilenko 1997).

Studies showed that the northern distribution of trees might already be expanding. Many investigators have reported vigorous tree regeneration owing to recent climatic warming (Brinks 1959; Payette and Filion 1985). For example, expansion of white spruce populations at the northern limit of distribution has occurred. This tree line lies along the east coast of Hudson Bay, and has expanded significantly over the last 100 years in response to warmer temperatures. During this period of time, the rapid white spruce expansion has produced a significant increase in tree density within preexisting forest stands, in newly formed groves and on sites where

isolated trees now grow (Payette and Filion 1985). The amount of new area invaded is relatively small. Theoretical calculations of temperate and boreal paleoecological data, which deals with the interactions between ancient organisms and their environment, suggest that it took tree populations between 50 and 1000 years to migrate 50 km from original locations in the past (Solomon and Kirilenko 1997). In addition, extra time would be needed for subsequent infilling of adjacent and available site for growth (Davis 1987 1990), and normal development of mature, closed-canopy forests (Shugart 1984). The minimum cumulative time from completion of these processes would range from 400 to >1850 years; this time span exceeds the 70-80 years projected for a climate with doubled CO_2 concentrations (Solomon and Kirilenko 1997).

During the next 70-80 years, tree populations could be extirpated from portions of their present geographic ranges as extant trees die (Franklin et al. 1987), and seedlings are unable to establish (Chambers and MacMahon 1994). Hogg and Hurdle (1995) suggest that if the predicted warming and drying occurs, one-half of the western Canadian boreal forests could be exposed to a drier climate similar to the present Aspen Parkland zone. Conifers are generally absent in this zone and aspen are restricted to patches of stunted trees interspersed with grasslands. If the Aspen Parkland is a dry-climate analogue for the future of the boreal forest as suggested by Hogg and Hurdle (1995), it would likely lead to a reduction in the productivity of commercial forest species in the southern boreal forest of Saskatchewan. The current southern limit of conifers in Saskatchewan is estimated to be climatically restricted by lack of moisture, preventing seedlings from establishing, therefore even a slight shift toward drier climatic conditions could have a significant impact on natural conifer distribution (Hogg 1994). On the other hand, if fire plays a more critical role in limiting present conifer distribution than moisture, these species may continue to persist and regenerate in the southern boreal forest under

significantly drier climates than present, provided there is no increase in fire frequency (Hogg 1994).

The distribution and abundance of species are governed by the birth, growth, death, and dispersal rates of individuals composing a population (Hansen et al. 2001). These individuals will react to climate change with a range of responses, and community composition will change in reaction to a complex set of factors such as climatic effects, disturbances, dispersal regimes, land use, and interspecific interactions (Hansen et al. 2001). Local, regional and global changes in temperature and precipitation can have large effects on the occurrence, timing, frequency, duration, extent, and intensity of disturbances (Baker 1995; Turner et al. 1998). These disturbances can include fire regime alterations, drought, introduced species, insect and pathogen outbreaks, windstorms, and ice storms (Dale et al. 2001) and can greatly shape the composition, structure and functioning of the forest ecosystem. This large variety of interplaying factors displays the complexity of interactions that will occur as climatic change continues.

The possible impacts of climate change on natural ecosystems can only be investigated using spatially distributed ecosystem process models that respond realistically to climatic factors (Price et al.1999). The most plausible forecasts of future climate originate from simulations carried out using General Circulation Models (GCMs) (Price et al.1999). Therefore, the climate change model chosen for use in this study is the second version of the Canadian Center for Climate Modeling and Analysis (CCCma) Canadian Global Climate Model version 2 (CGCM2). This model is based on an earlier version called CGCM1, with many improvements (http://www.cccma.bc.ec.gc.ca/models/cgcm2.shtml). The CGCM2 uses the same atmospheric components as CGCM1, but has improved ocean mixing parameterization and sea-ice dynamics. A comparison of CGCM1 and CGCM2 can be found in Flato and Boer (2000)

(http://www.cccma.bc.ec.gc.ca/models/cgcm2.shtml). The CGCM's main drawback is their coarse resolution relative to similar models such as Canadian Regional Climate Models (CRCMs).

The CGCM2 has been used with the Intergovernmental Panel on Climate Change's Special Report on Emissions Scenarios (IPCC SRES) A2 and B2 (http://www.cccma.bc.ec.gc.ca/models/cgcm2.shtml). The IPCC SRES A2 and B2 forcing scenarios span the time period 1990 to 2100, and take two different approaches to estimating GHG emissions in the future. The A2 scenario predicts a future population reaching 15 billion by the year 2100. This scenario has slow economic and technological development (http://www.cccma.bc.ec.gc.ca/data/cgcm/cgcm_forcing.shtml). The B2 scenario, on the other hand, envisions a slower population growth (10.4 billion by 2100) with a more rapidly evolving economy and emphasis placed on environmental protection. Therefore, this emission scenario produces lower emissions and less warming (http://www.cccma.bc.ec.gc.ca/data/cgcm/cgcm_forcing.shtml).

Although climate change models still have many discrepancies, it is still safe to conclude that the rate of change and magnitude of warming over the next century could be within the expected range shown by models or even higher (Hengeveld 2000). This warming trend can in turn have profound effects on natural ecosystems and human society that will have difficulties adapting to this rate of climate change (Hengeveld 2000).

3.0 MATERIALS AND METHODS

3.1 Study Area

The Saskatchewan Mixedwood Forest extends in a 35 to 285 km-wide band across the province, in a southeast direction between approximately 52° and 56° north latitude (Canadian Forest Service 1986). This area (about 11,564 $km^{2)}$ is composed of three distinct Ecoregions including the Mid-boreal Upland, the Mid-boreal Lowland and the Boreal Transition. Collectively these Ecoregions are the Boreal Plain Ecozone (Canadian Forest Service 1986). The sites used for this study are restricted to the Mid-boreal Upland and Boreal Transition Ecoregions. Generally, the Mixedwood Forest is characterized by gently rolling, glacial plain with elevations from 305 to 815 m above sea level. Climate ranges from sub-humid to cool continental climate, with short, warm summers and long, cold winters. The mean January temperature is -20°C while that in July temperature averages 17°C (Canadian Forest Service 1986).

3.2 Seed Sources

White spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (P. Mill) B.S.P), and jack pine (*Pinus banksiana* Lamb.) were studied. Seeds of these trees were obtained

from the Weyerhaeuser Seed Orchard, north of Prince Albert, Saskatchewan. Seed collections consisted of 12 populations for white spruce and black spruce, and 10 populations for jack pine (Tables 3.1-3.3; Figure 3.1-3.3). Seeds were stored at –18ºC until used in experiments.

Seeds were collected from natural populations. White spruce seeds were collected from trees using a cone rake. Cones were dumped in a truck and taken to a central location where they were hand sorted. Woodlots where seeds collected were approximately 3 ha in size. Cones were then stored in a refrigerated van and taken to Pacific Regeneration Technologies Inc. (PRT) for extraction, testing, and storage (L. Corriveau 2005, personal communication).

Black spruce tree tops were collected from harvested trees in cutover areas and transported to a central location and hand picked. Cones were stored on site, and then delivered to the Weyerhaeuser Seed Orchard north of Prince Albert, Saskatchewan. Cones were delivered to PRT for extraction, testing, and sorting (L. Corriveau 2005, personal communication).

Jack pine cones were picked from the tops of trees in cutover landings during the winter. Cones were stored in burlap sacks and transported to the extraction facility at PRT, north of Prince Albert, Saskatchewan. The seeds were then extracted, tested, and stored at this facility (L. Corriveau 2005, personal communication).

Table 3.1. Locations and site characteristics of 12 white spruce (*Picea glauca*) populations from the Boreal Plain Ecozone in Saskatchewan.

Collection #	Location	Latitude/ Longitude	Ecoregion	Landscape area	Dominant soil type	Soil texture
1	Riley's Bluff	54º14.4´4.09´´N 105º55´13.9´´W	Mid-Boreal Upland	Montreal Lake Plain	Gray Luvisolic	Sandy Loam
2	Clark Tower	54º29´27.4´´N 107º0´25.4´´W	Mid-Boreal Upland	Clarke Lake Plain	Organic	Loamy
3	Tracey East	54º30´18.5´´N 105º46´19.8´´W	Mid-Boreal Upland	Montreal Lake Plain	Gray Luvisolic	Sandy Loam
4	Dunbar	54º40´14.1´ºN 107º0´57.3´´W	Mid-Boreal Upland	Smoothstone Plain	Gray Luvisolic	Loamy
5	Mile 31, Hwy#9	53º13´7.6´´N 102º18´14.1´´W	Mid-Boreal Upland	Pasquia Encarpment	Gray Luvisolic	Loamy
6	Ruby lake	52º57´9.5´´N 102º28´9.8´´W	Boreal Transition	Hudson Bay Plain	Dark Gray Chernozemic	Loamy
7	Kenney Lake	52º19´14.8´´N 102º21´31.9´´W	Mid-Boreal Upland	Porcupine Plains	Gray Luvisolic	Loamy
8	Paddockwood	53º25´39.1´´N 105º36´7.2´´W	Boreal Transition	Shellbrook Plain	Dark Gray Chernozemic	Loamy
9	Prairie River	52º51´57.2´´N 102º37´22.9´´W	Boreal Transition	Hudson Bay Plain	Gray Luvisolic	Loamy
10	Greenbrush	52º52´17.3´´N 102º55´11.8´´W	Boreal Transition	Hudson Bay Plain	Gray Luvisolic	Loamy
11	Tolko	53º56´0.5´´N 107º53´39.6´´W	Boreal Transition	St. Cyr Plain	Gray Luvisolic	Loamy
12	Bainbridge	53º29´4.59´´N 102º8´10.8´´W	Mid-Boreal Upland	Pasquia Encarpment	Gray Luvisolic	Loamy

Table 3.2. Locations and site characteristics of 12 black spruce (*Picea mariana*) populations from the Boreal Plain Ecozone in Saskatchewan.

Collection #	Location	Latitude/ Longitude	Ecoregion	Landscape area	Dominant soil type	Soil texture
1	Access/Besnard	54º46´32.2´´N 105º37´18.6´´W	Mid-Boreal Upland	La Ronge Lowland	Brunisolic	Sandy
2	Clark's Road	52º19´26.2´´N 102´30´19.6´´W	Mid-Boreal Upland	Porcupine Hills	Gray Luvisolic	Loamy
3	Weyakwin	54º24´51.1´´N 105º55´28.4´´W	Mid-Boreal Upland	Waskesiu Upland	Gray Luvisolic	Loamy
4	Lorenz Lake Road	54º3´29.6´´N 105º0´0´´W	Mid-Boreal Upland	Whiteswan Upland	Gray Luvisolic	Sandy Loam
5	Two Forks	54º41´1.6´´N 105º55´50.4´´W	Mid-Boreal Upland	Waskesiu Upland	Gray Luvisolic	Sandy Loam
6	Smoothstone	54º45´46.3´´N 106º51´54.2´´W	Mid-Boreal Upland	Clarke Lake Plain	Gray Luvisolic	Loamy
7	Circle Drive	54º29´44.4´´N 106º41´54.4´´W	Mid-Boreal Upland	Clarke Lake Plain	Gray Luvisolic	Loamy
8	Vimy	53º45´39´´N 107º34´44.3´´W	Boreal Transition	St. Cyr Plain	Brunisolic	Sandy
9	Big Horn	52º13´13.2´´N 102° 4' 28.0´´ W	Mid-Boreal Upland	Porcupine Hills	Gray Luvisolic	Loamy
10	Bannock	52º52´34.7´´N 103º13´0.9´´W	Boreal Transition	Mistatim Upland	Gray Luvisolic	Clayey
11	Evenden	53°47'15.8"N 104°32'40.7´´W	Mid-Boreal Upland	White Gull Plain	Brunisolic	Sandy
12	Mile 47 Hwy#9	53º29´4.59´´N 102º8´10.8´´W	Mid-Boreal Upland	Pasquia Encarpment	Gray Luvisolic	Loamy

Table 3.3. Locations and site characteristics of the 10 jack pine (*Pinus banksiana*) populations from the Boreal Plain Ecozone in Saskatchewan.

Collection #	Location	Latitude/ Longitude	Ecoregion	Landscape area	Dominant soil type	Soil texture
1	Elaine Lake	54º24′28.4′′N 106º32′26.6′′W	Mid-Boreal Upland	Waskesiu Uplands	Gray Luvisolic	Loamy
2	Bird Lake	53º47′10.3′′N 105º45′32.1′′W	Mid-Boreal Upland	Montreal Lake Plain	Gray Luvisolic	Loamy
3	Fir River	53º8′17.7′′N 102º45′32.1′′W	Mid-Boreal Upland	Pasquia Plateau	Organic	Loamy
4	Mile 47-Hwy#9 (Mountain Cabin)	53º29′4.6′′N 102º8′10.8′′W	Mid-Boreal Upland	Pasquia Encarpment	Gray Luvisolic	Loamy
5	Fir River	52º51′57.2′′N 102º37′22.9′′W	Boreal Transition	Hudson Bay Plain	Gray Luvisolic	Loamy
6	Dahl River	53º2′32.8′′N 102º27′50.9′′W	Boreal Transition	Hudson Bay Plain	Dark Gray Chernozemic	Loamy
7	Greenbush	52º52′7.6′′N 102º46′17.3′′W	Boreal Transition	Hudson Bay Plain	Gray Luvisolic	Loamy
8	Greenbush	52º46′44.2′′N 102º46′33.8′′W	Boreal Transition	Hudson Bay Plain	Gray Luvisolic	Loamy
9	Tobin Lake Area	53º35′50.2′′N 103º20′16.1′′N	Boreal Transition	Nipawin Plain	Dark Gray Chernozemic	Clayey
10	Henribourg	53º25′39.1′′N 105º36′7.2′′W	Boreal Transition	Shellbrook Plain	Dark Gray Chernozemic	Loamy

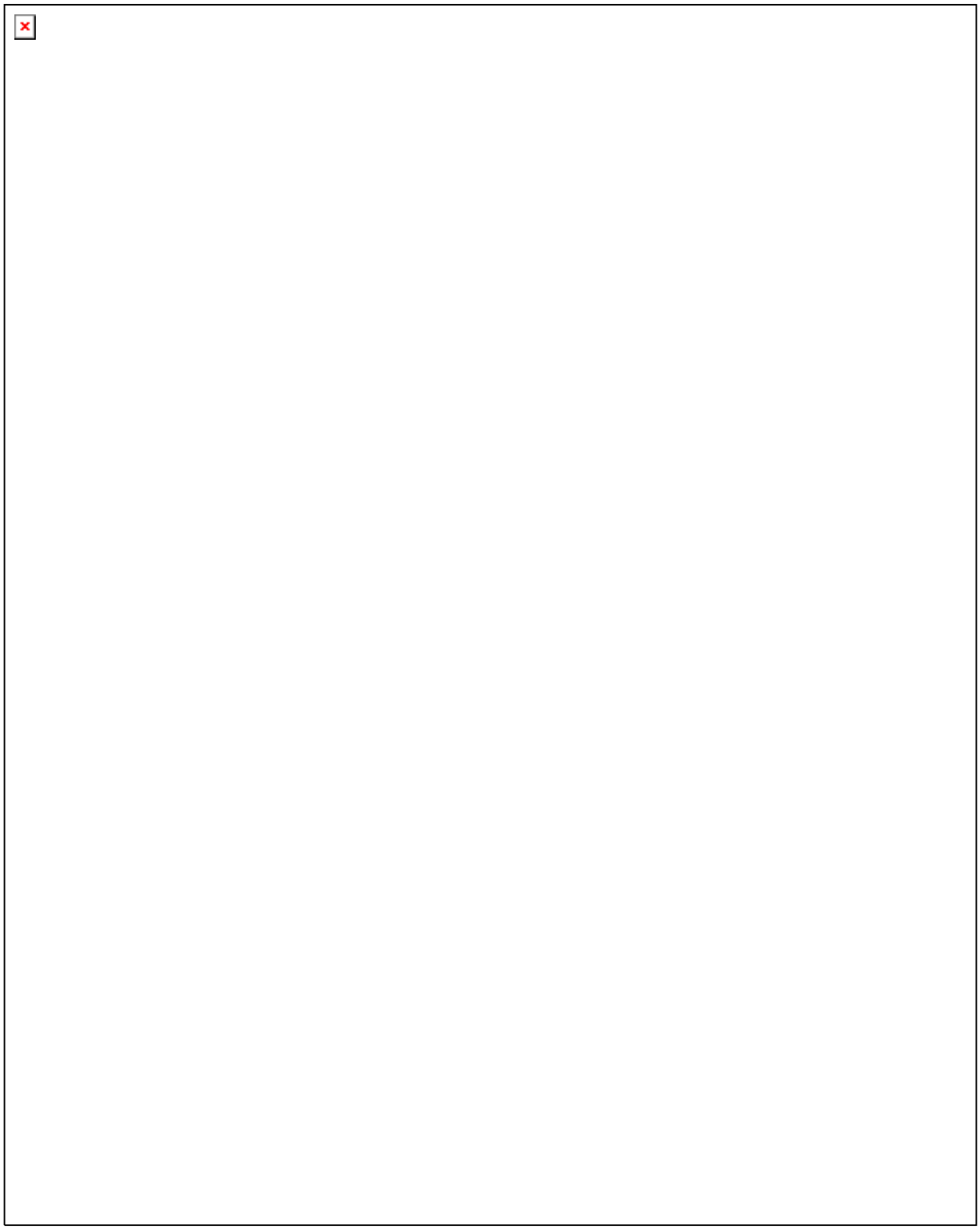

Figure 3.1: Geographic locations of white spruce (*Picea glauca*) seed collections in the Boreal Plain Ecozone Saskatchewan.

Figure 3.2: Geographic locations of 12 black spruce (*Picea mariana*) seed collections in the Boreal Plain Ecozone of Saskatchewan.

Figure 3.3: Geographic locations of jack pine (*Pinus banksiana*) seed collections in the Boreal Plain Ecozone of Saskatchewan.

3.3 Experiment 1: Influences of light and cold stratification on dormancy and germination

3.3.1 Experimental design and germination tests

A Completely Randomized Design (CRD) with five replicates was used to determine dormancy-breaking requirements of these trees. Two factors used in this experiment were light (light or darkness) and stratification (stratified or unstratified).

Each experimental unit had 50 seeds placed on two sheets of Whatman® Number 1 filter paper in 9 cm plastic Petri dishes. Before stratification, filter paper was moistened with 5 mL of distilled water. Petri dishes were placed in clear ziplock bags, and covered by black plastic bags to reduce water loss and avoid exposure to light. Petri dishes were placed in a cold room held at 4°C for 21 days in complete darkness. Seeds were checked weekly and a 0.05% benomyl solution was sprayed on seeds when any sign of fungal infection appeared (Qiu et al. 2006). Unstratified seeds were used as the control.

Stratified and non-stratified seeds were split and subjected to light or darkness treatment giving four combinations of light and stratification: 1) Stratified/Light, 2) Stratified/Dark, 3) Unstratified/Light, and 4) Unstratified/Dark. The light treatment consisted of 12 hours of light and 12 hours of darkness. Seeds were incubated in a growth chamber at 25°C, the optimal germination temperature for most conifer species (Farmer 1997). Germinated seeds were counted and removed from the Petri dishes once a week. Seeds were considered germinated when the radicle was ≥2 mm. Seeds were visually examined for fungal infections during germination checks; a 0.05% benomyl solution was applied if infections were discovered. Distilled water was added when necessary to keep the filter paper moist. Most seeds of jack pine and black spruce germinated after four weeks, white spruce after seven weeks. Germination tests

were terminated after 100% germination was reached or after 2 weeks without additional germination.

3.3.2 Data Analysis

Percent germination was transformed using arcsine square root transformations (Zar 1984). Analysis of variance (ANOVA) in SAS 9.1.3 (SAS Institute Inc. 2003) was used to determine the effect of stratification and light on germination and dormancy within each seed collection. The threshold for significance was held at P=0.05. Data with interactions among stratification and light treatments were subject to further analysis by using a one-way ANOVA to examine the effects of light and stratification. Results from this experiment were used to determine the germination conditions for the thermal time model.

3.4 Experiment 2: Seed germination tests for thermal time model application

3.4.1 Experimental design and germination test

A randomized complete block design (RCBD) was used determine the germination requirements of white spruce, black spruce and jack pine seeds. Five replicates were started at weekly intervals, and considered as blocks. Seven Sanyo Versatile Environmental Test Chambers were used in the first stage of the experiment. Each chamber was assigned a constant temperature of 5, 10, 15, 20, 25, 30, or 35 °C. Conditions within each chamber consisted of 12/12 hours light/darkness.

Each experimental unit consisted of 25 seeds placed on two sheets of Whatman ® No. 1 filter paper moistened with 5 mL of distilled water in 9 cm plastic Petri dishes. Petri dishes were enclosed in clear plastic bags to reduce evaporation, and then randomly placed in growth chambers at each temperature. Petri dishes were placed on three middle shelves in each growth chamber and temperatures were recorded on each of the shelves to obtain temperature measurements for the entire chamber. Temperatures within each chamber were recorded hourly

using a Campbell scientific 21X data logger. During the course of the experiment, seeds with any sign of fungal infection were treated with 0.05% benomyl solution. Seeds were treated with 95% ethanol (Wang et al. 2004), because it more effectively fungal infections on conifer seeds. Distilled water was added periodically when the filter paper became dry. Germinated seeds were counted and removed every 24 hours for approximately 30-100 days depending on temperature and species. Seeds were considered germinated when the radicle was ≥ 2mm in length.

Temperatures of 5 and 10°C produced low germination for all conifer species, and a thermal time model could not be constructed. Therefore, two temperatures, 12.5 and 17.5°C, were added for germination testing. Only white spruce and black spruce seed collections were used for these additional temperatures due to shortage of seeds in jack pine collections.

3.4.2 Tetrazolium Testing (TZ)

Tetrazolium tests were conducted for all seed collections, following procedures established by the International Seed Testing Association (1985) and Grabe (1970). Five replicates, each consisting of 25 seeds, were used for each seed collection. Seeds were moistened with distilled water at room temperature (about 20oC) by soaking white spruce and black spruce seeds for 20 hours; jack pine seeds were soaked in water for 18 hours. Seeds were removed from Petri dishes after the set time, and a transverse cut was made on both ends of the seeds. This cut was big enough to ensure that the inner seed coat was broken without causing major injury to the embryo (International Seed Testing Association 1985). This technique exposes the internal tissues of conifer seeds, allowing easier penetration of the tetrazolium solution. Seeds were kept moist throughout this procedure, then transferred to a Petri dish where an aqueous solution of 1%, 2,3,5-triphenyltetrazolium bromide was added until seeds were completely immersed. These Petri dishes were immediately transferred to a dark room, and held

at room temperature for 24 hours. Complete darkness was used because direct light causes a reduction in the tetrazolium salt (International Seed Testing Association 1985). Each individual seed was then sliced open and examined. Seeds that stained completely bright red were considered viable. Seeds that did not stain completely or revealed an uncharacteristic coloring and/or flaccid essential structures were considered non-viable.

3.4.3 Calculation of the degree of dormancy

Viable seeds can germinate and produce a normal plant under appropriate germination conditions. Viability percentages for each seed collection were based on results from tetrazolium tests (n=5). These values were then used to determine the degree of dormancy for each collection. The degree of dormancy describes the percentage of dormant seeds from each collection. Seeds that germinated under non-stratified and dark conditions at 25°C were considered non-dormant. Germination percentages were then subtracted from viability percentages to give the degree of dormancy for each collection. When negative numbers were obtained (actual germination> viability), these values were changed to zero.

3.4.4 Procedures for thermal time model application

Cumulative germination was calculated for each collection at each temperature. All values were then transformed by a scaling factor into proportions (Ellis et al. 1986). The scaling factor was obtained by multiplying the number of seeds by the viability based on the TZ test. The scaling factor adjusted the germination percentage for each seed collection by taking into account the actual viability of each collection. The transformed data of all replicates within each temperature and collection were regressed using the Chapman-Richards function (Richards 1959; SigmaPlot 2005):

$$y = a(1-e^{-bx})^c \qquad (3.1)$$

where y = germination percentage, x = time, a = the asymptote, b = the rate parameter, and c = the shape parameter (Qiu et al. 2006). This sigmoidal equation was used to model the germination time course for each collection, temperature, and replicate. Three parameters (a, b, and c) were estimated using a curve fitter program in Sigmaplot by varying all the parameters until the closest fit for the data was produced (SigmaPlot 2005; Appendix C).

Seed populations were considered to be composed of subpopulations (10, 20, 30, 40, 50, 60, 70, 80, and 90%) based on relative germination rate to facilitate modeling purposes (Garcia-Huidobro et al. 1982; Hardegree and Van Vactor 1999). These percentile rankings were assumed to represent subpopulations that would germinate in the same relative order regardless of thermal conditions (Garcia-Huidobro et al. 1982; Hardegree and Van Vactor 1999). The number of days required to achieve 10-90% germination was calculated from the modeled germination time course based on the Chapman-Richards function. A non-linear regression procedure in SAS (Proc NLIN) was used to estimate germination time $t_{(g)}$ for the 10, 20, 30, 40, 50, 60, 70, 80, and 90% subpopulations where available (Qiu et al. 2006).

The formula by Garcia-Huidobro et al. (1982) was then used to determine the germination rate (GR) of each collection:

$$GR(g) = 1/t(g) = (T-Tb)/\theta T(g) \qquad (3.2)$$

where GR(g) is the reciprocal of germination time (tg) to a given germination percentile (g), which is assumed to be linearly related to temperature (T) within the sub-optimal range between base temperature (Tb) and optimal temperature (T_o) for non-dormant seeds (Wang et al. 2004).

The range of T_b to T_o (sub-optimal temperature range) allows germination timing to be described on the basis of thermal time or heat units, and within this range thermal time can be used to compare germination between species (Garcia-Huidobro et al. 1982). The range of sub-optimal temperatures was established based on visual inspection of the linear relation between germination rate and temperature (Wang et al. 2004; Qiu et al. 2006). Values that deviated from a linear relationship were excluded from the calculations, and were considered to be supra-optimal temperatures. Subpopulations containing a single value in the sub-optimal temperature range were excluded from the calculation of base temperature and thermal time. Germination rate for each subpopulation was plotted against temperature and the base temperature was estimated using graphical extrapolation techniques (Garcia-Huidobro et al. 1982; Qiu et al. 2006) assuming a single base temperature for all sub-populations. The intercept of the linear regression line is T_b, and the slope of the regression line is the thermal time ($\theta T_{(g)}$).

If the variation of $\theta T_{(g)}$ within a seed population follows a normal distribution, the germination time course in terms of thermal time can be described by (Ellis et al. 1986; Wang et al. 2004):

$$\text{Probit}(g) = \frac{(T - T_b) * t_{(g)} - \theta T_{(50)}}{\sigma_{\theta T}} \qquad (3.3)$$

Cumulative germination percentage is transformed using log10 Probit to linearize percentage data (Finney 1971; Wang et al. 2004). In this formula, $\theta_{T(50)}$ is the median thermal time for the 50% sub-population, and the standard deviation of thermal time ($\sigma_{\theta T}$) is the reciprocal of the linear regression slope of Probit germination for all sub-populations (Wang et al. 2004) or standard deviation of thermal time. Probit analysis was then used to estimate $\theta_{T(50)}$ and $\sigma_{\theta T}$ for each seed collection, and used in the application of the thermal time model.

3.5 Relating germination parameters to predicted climate in the future

Temperatures (1961-1990) for the study area were obtained from the Canadian Soil Information System (CanSIS) database (http://www.brocku.ca/maplibrary/digital/Cansis.htm). Monthly average temperature was available for each Ecodistrict within Saskatchewan, and temperatures were obtained for each collection based on closest Ecodistrict. Ecodistricts were matched to sites where seeds were collected using longitude and latitude coordinates.

The Canadian Global Climate Model, version 2 (CGCM2) was chosen to obtain predicted temperature and precipitation for 2020, 2050, and 2080. This model is available through the Intergovernmental Panel on Climate Change (IPCC) (http://ipcc-ddc.cru.uea.ac.uk/index.html). Monthly minimum and maximum temperatures and precipitation (mm) for the sites where seeds were collected were obtained and used to calculate monthly averages. IPCC has created a range of scenarios that vary with future projected human population size, energy use, technology, and other factors influencing anthropogenic gas emissions (Goldblum and Rigg 2005). Climate models are highly sensitive to human behavior, therefore two different emission scenarios, A2 and B2, were chosen to represent a different emission strategy and future global population. The worse case scenario (A2) assumes high concentrations of carbon dioxide emissions that represent a future with little modification to human behavior and population growth (Goldblum and Rigg 2005). The B2 scenario assumes significant environmental protection, slower population growth, and lower emissions (Goldblum and Rigg 2005).

A graphical presentation that includes current and future temperatures and precipitation, along with base temperature for each seed collection, was used to determine possible timing of seed germination in the field under current and future temperature regimes. Time periods with temperatures higher than the base temperature were estimated under current and predicted temperatures in the future for the A2 and B2 scenarios.

3.6 Linking base temperatures, $\theta T_{(50)}$ and degree of dormancy to geographic locations, temperature and precipitation

Using SAS (Proc Corr) analysis, base temperatures, $\theta T_{(50)}$ and degree of dormancy for each species were correlated with latitude, longitude, current temperatures and precipitation (1961-1990) for each site where seeds were collected. Average temperatures in April, May, June, the annual mean temperature, and corresponding precipitation were chosen for the analysis.

4.0 RESULTS

4.1 Influences of light and cold stratification treatments on dormancy and germination

4.1.1 White spruce

Both light and stratification treatments affected final seed germination percentage in most white spruce collections, but the interaction between light and stratification was significant in four collections (1, 3, 6, and 7) (Table 4.1). Data were further analyzed within each factor for those collections. Within the stratification treatments for Collections 1 and 3, no significant difference was found in final germination between light and dark treatments. Without stratification, germination was higher under light than in darkness. Within the light treatment, germination was not significantly different between stratification treatments. Under darkness, stratification produced higher germination relative to the non-stratified treatment. A different trend occurred in Collections 6 and 7 wherein germination increased with stratification and light. Without stratification, no difference existed in germination between light and dark treatments. Within the light treatments, germination was not different between stratification treatments. Stratification decreased germination in darkness.

Stratification increased germination for Collections 2 and 10, but reduced germination in Collections 8 and 9 under light and darkness. Collections 4, 5, 11, and 12 were not affected by stratification (Table 4.1, Figure 4.1). Light improved germination in Collections 2, 5, 8, and 10 in stratified and non-stratified treatments, and Collections 6 and 7 with stratification. Light did not reduce germination for any collection, and had no effect on germination for Collections 4, 9, 11, and 12.

Germination of white spruce collections across Saskatchewan's Boreal Plain Ecozone had a mixed response to stratification and light treatments. Such diverse effects make it impossible to choose an overall treatment method that would improve germination among collections.

Table 4.1. Probabilities that stratification, light, and their interactions affected seed germination of 12 white spruce collections. Significant effects are highlighted (P≤0.05).

	Treatment		
Collection	Stratification (St)	Light (L)	St*L
1	**0.04**	0.27	**0.00**
2	**0.01**	**0.00**	0.33
3	0.09	0.80	**0.01**
4	0.43	0.79	0.28
5	0.54	**0.00**	0.86
6	**0.00**	**0.00**	**<.0001**
7	**0.05**	**0.02**	**0.02**
8	**0.05**	**0.02**	0.95
9	**<.0001**	0.57	0.32
10	**0.00**	**0.00**	0.33
11	0.64	0.28	0.30
12	0.64	0.42	0.29

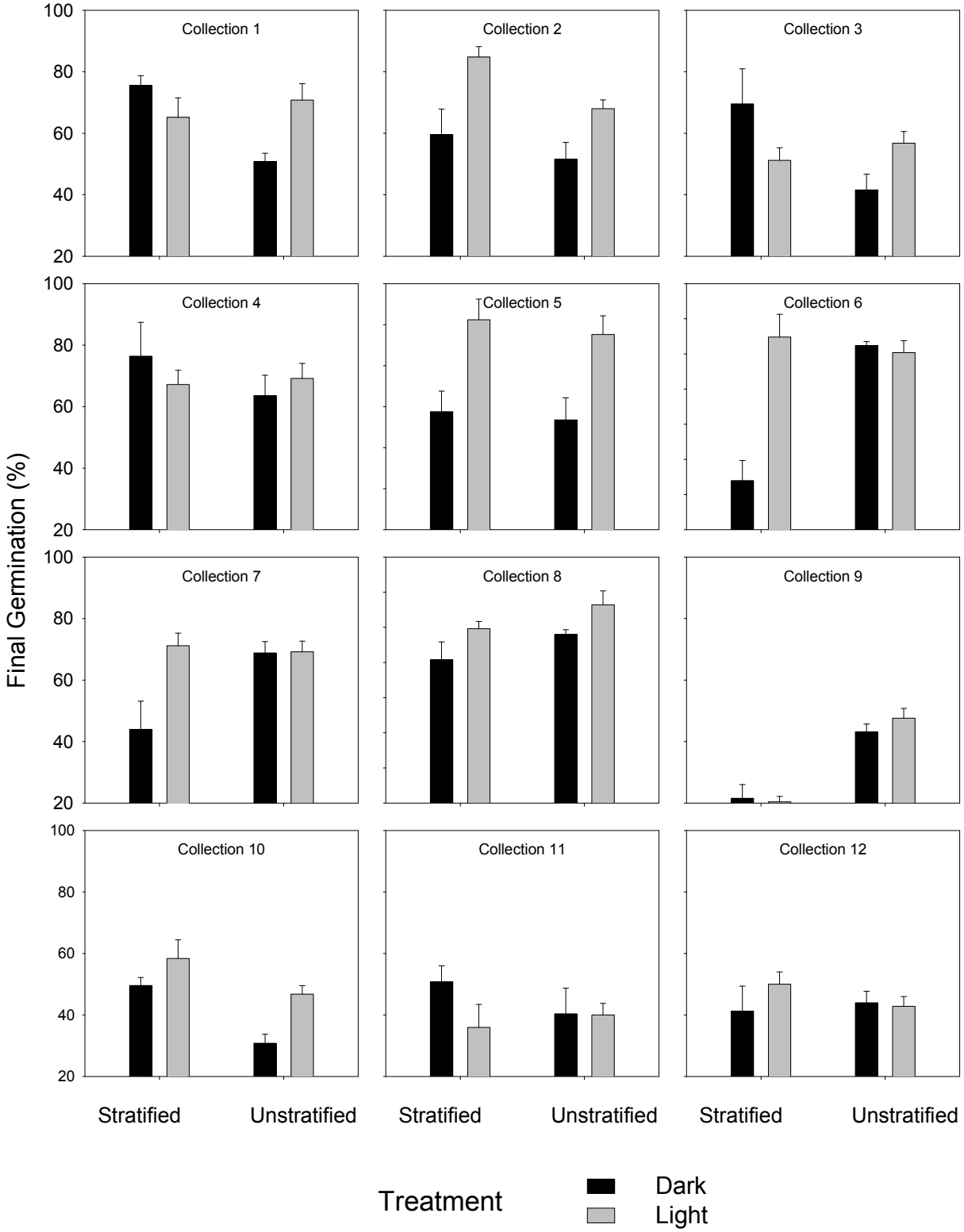

Figure 4.1. Influences of light and cold stratification on germination for 12 white spruce collections from the Boreal Plain Ecozone of Saskatchewan. Bars are means + SD.

4.1.2 Black spruce

Black spruce had high germination across all collections, ranging from 76-100% (Figure 4.2). The majority of black spruce collections showed no response to stratification, except for Collections 2, 7, and 9 in which germination was reduced by stratification (Table 4.2). No interactive effects were found between stratification and light, and light had no significant effect on germination. Therefore, black spruce collections from the Boreal Plain Ecozone of Saskatchewan had low dormancy and did not require light or stratification to break dormancy.

Table 4.2. Probabilities that stratification, light, and their interactions affected seed germination of 12 black spruce collections. Significant effects are highlighted (P≤0.05).

	Treatment		
Collection	Stratification (St)	Light (L)	St*L
1	0.08	0.34	0.29
2	**0.00**	0.65	0.37
3	0.08	0.08	0.87
4	0.11	0.47	0.94
5	0.50	0.47	0.28
6	0.13	0.64	0.57
7	**0.00**	0.62	0.87
8	0.43	0.32	0.43
9	**0.05**	0.24	0.24
10	0.06	0.79	0.11
11	0.68	0.18	0.30
12	0.38	0.54	0.45

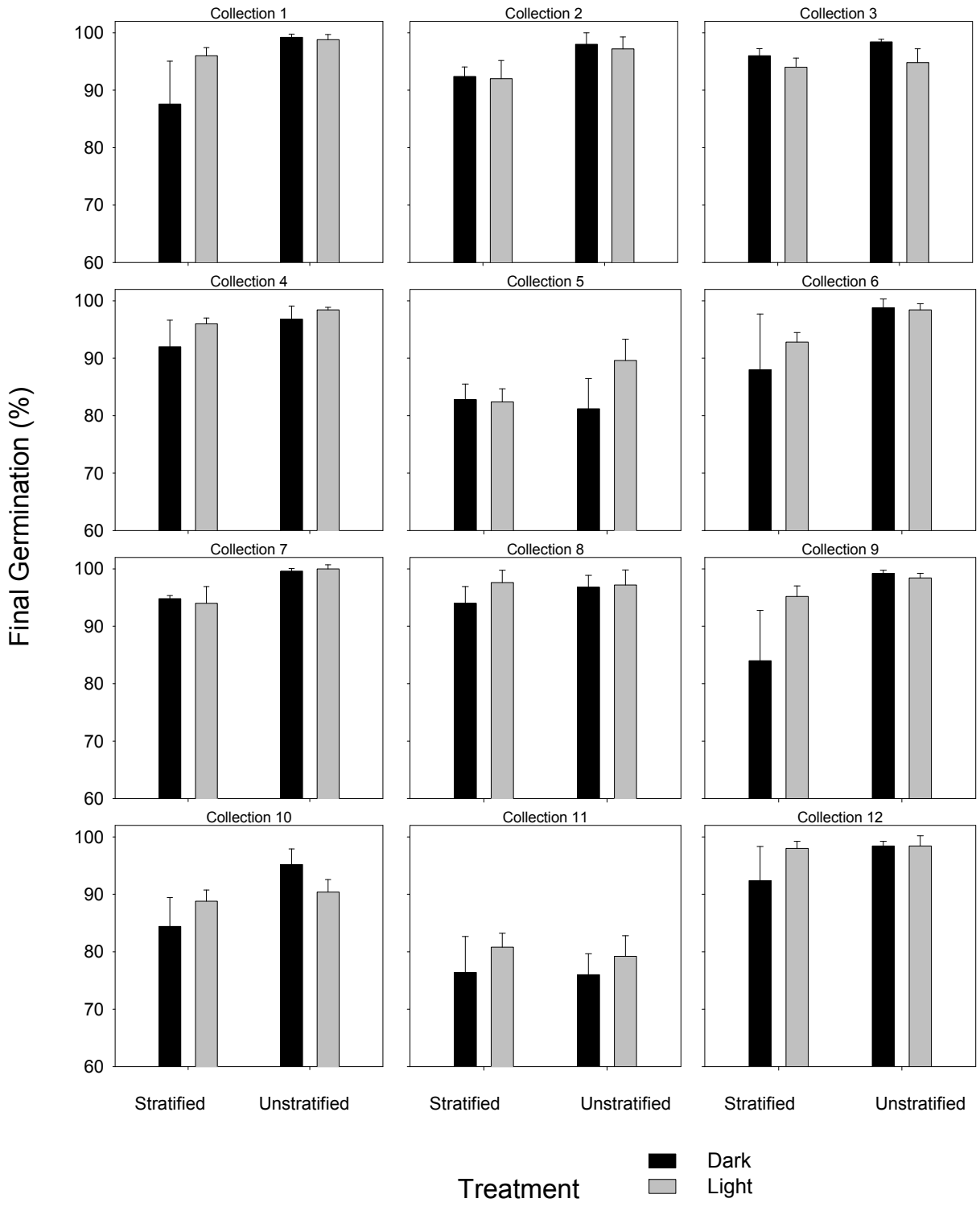

Figure 4.2. Influences of light and cold stratification on germination for 12 black spruce collections from the Boreal Plain Ecozone of Saskatchewan. Bars are means + SD.

4.1.3 Jack pine

Light and/or stratification treatments affected seed germination for all jack pine collections, but the interaction between light and stratification was significant in Collections 2, 4, 5, and 10 (Table 4.3). For Collections 2 and 5 no significant difference appeared in germination between light and dark within the stratification treatment. Without stratification, germination was higher under light than in darkness. Within the light treatment, no significant difference occurred in germination between stratification treatments. Stratification improved germination in darkness. Germination of Collection 4 was not significantly affected by light. Stratification reduced germination under light, but had no significant effect on germination in darkness. In Collection 10, stratification augmented germination in darkness; without stratification, differences in germination between light and dark treatments were not apparent. Under light, non-stratification conditions had superior germination, but in darkness no significant difference occurred in germination.

Stratification reduced germination in Collections 1, 7, and 8, but had no significant effect on Collections 3 and 6. Stratification increased germination in Collection 9 in darkness. Light improved germination for Collection 3, and reduced germination in Collection 6. Collections 1, 7, and 8 were unaffected by light. Light augmented germination of non-stratified seeds in Collection 9.

Overall, jack pine seeds showed mixed response to stratification and light treatments. No single treatment can be used to enhance germination for all collections.

Table 4.3. Probabilities that stratification, light, and their interactions affected seed germination of 10 jack pine collections. Significant effects are highlighted (P≤0.05).

	Treatment		
Collection	Stratification (St)	Light (L)	St*L
1	**<.0001**	0.46	0.76
2	**0.02**	**0.00**	**0.01**
3	0.16	**0.03**	0.10
4	**0.03**	0.75	**0.02**
5	0.10	0.23	**0.01**
6	0.15	**0.03**	0.92
7	**0.01**	0.82	0.18
8	**0.03**	0.27	0.43
9	**0.03**	**0.05**	0.06
10	**0.04**	**0.00**	**0.00**

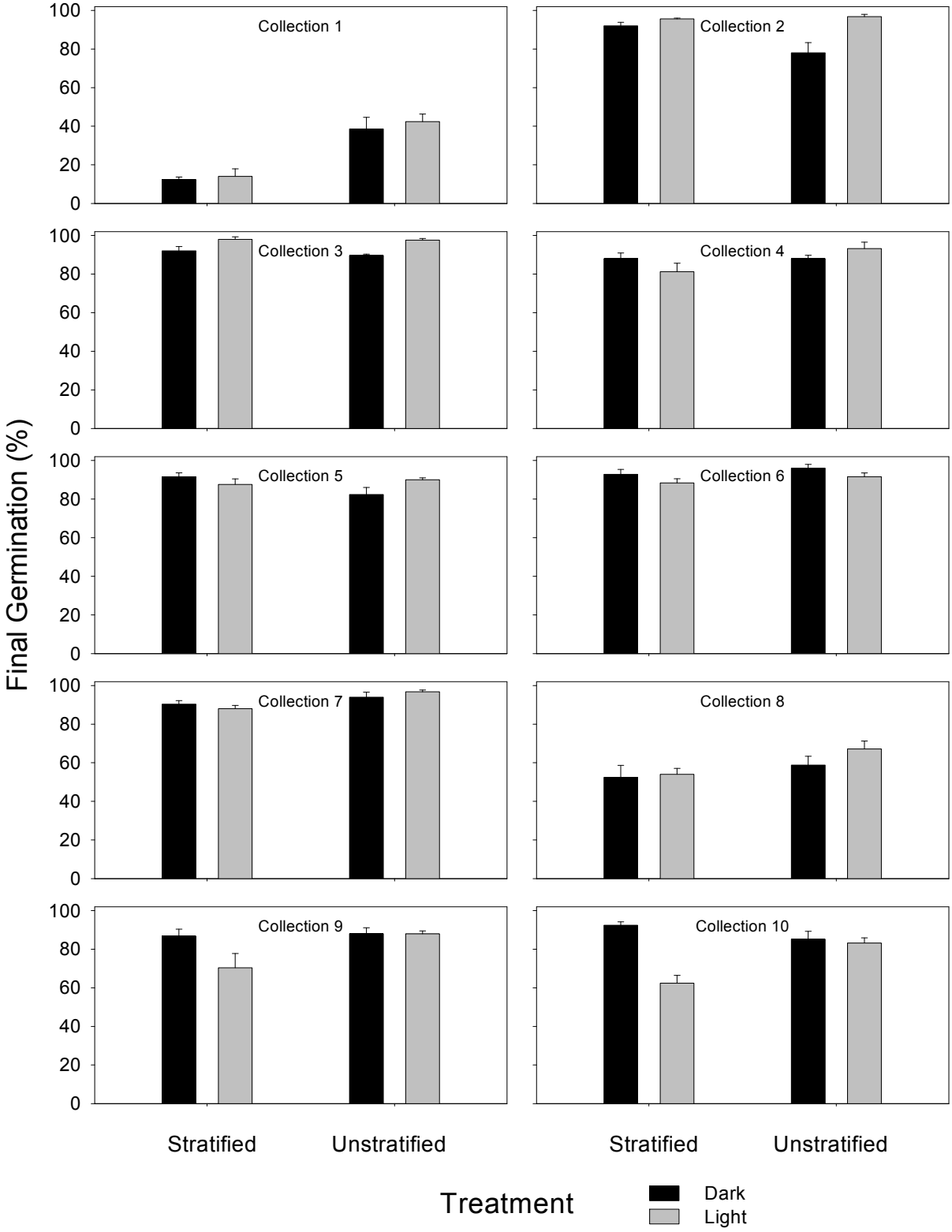

Figure 4.3. Influences of light and cold stratification on germination for 10 jack pine collections from the Boreal Plain Ecozone of Saskatchewan. Bars are means + SD.

4.1.4 Viability, the degree of dormancy, and the effect of temperature on germination

Most collections showed high seed viability (>80%) (Table 4.4). Jack pine Collection 1 had the lowest viability (73%). This suggested poor seed quality, as many seeds were chipped and prone to fungal infections during germination. This collection also had low germination.

The percentage of dormant seed was calculated using viability and germination percentage under optimal conditions (25°C, non-stratified, and darkness) (Table 4.4). These conditions were chosen based on the assumption that stratification and light do not break seed dormancy, and therefore only non-dormant seeds would germinate.

White spruce collections had the highest percentage of dormant seeds among tree species (Table 4.4). Over 50% of the seeds were dormant in Collections 3, 10, and 12. Black spruce showed little or no dormancy in the majority of seed collections. Highest dormancy among black spruce collections was 12% for Collection 5. Dormancy in jack pine seeds was intermediate between white spruce and black spruce. Jack pine also had the largest range of variation in dormancy among seed collections, from non-dormant (Collection 6) to 34% dormancy in Collection 1. Most jack pine seeds had low dormancy, with less than 24% in all but one collection. High dormancy in Collection 1 may be due to the low final germination percentage caused by poor seed quality.

Final germination over temperatures 5-35°C is shown for white spruce, black spruce, and jack pine in Figure 4.4. White spruce collections had high variability in germination among collections; most variable germination occurred at 17.5 and 25°C, and germination was reduced below 10°C or above 30°C. Black spruce had less variation in germination among collections with high germination between 17.5-30°C and decreased germination below 10°C or above 30°C. Jack pine germination increased from 15 to 20°C, and remained high until 30°C in most

of collections. Germination decreased sharply from 30-35°C, but was higher than white spruce and black spruce.

Table 4.1. Percentage of viable and dormant seeds for white spruce, black spruce and jack pine seed collections calculated using viability and germination percentage at 25°C in darkness without stratification.

Collection #	White spruce		Black spruce		Jack pine	
	Degree of Dormancy (%)	Viability (%)	Degree of Dormancy (%)	Viability (%)	Degree of Dormancy (%)	Viability (%)
1	48	98	0	98	34	73
2	37	89	0	95	18	96
3	52	94	2	100	2	91
4	33	97	0	94	4	92
5	45	92	12	93	14	96
6	27	99	0	91	0	95
7	29	98	0	100	4	98
8	30	98	2	99	24	82
9	43	86	0	98	9	97
10	53	84	4	99	4	90
11	48	88	10	86	-	-
12	53	97	2	100	-	-
Mean ±SD	42±9.8	93±5.3	3±4.0	96±4.5	11±11.0	91±7.1

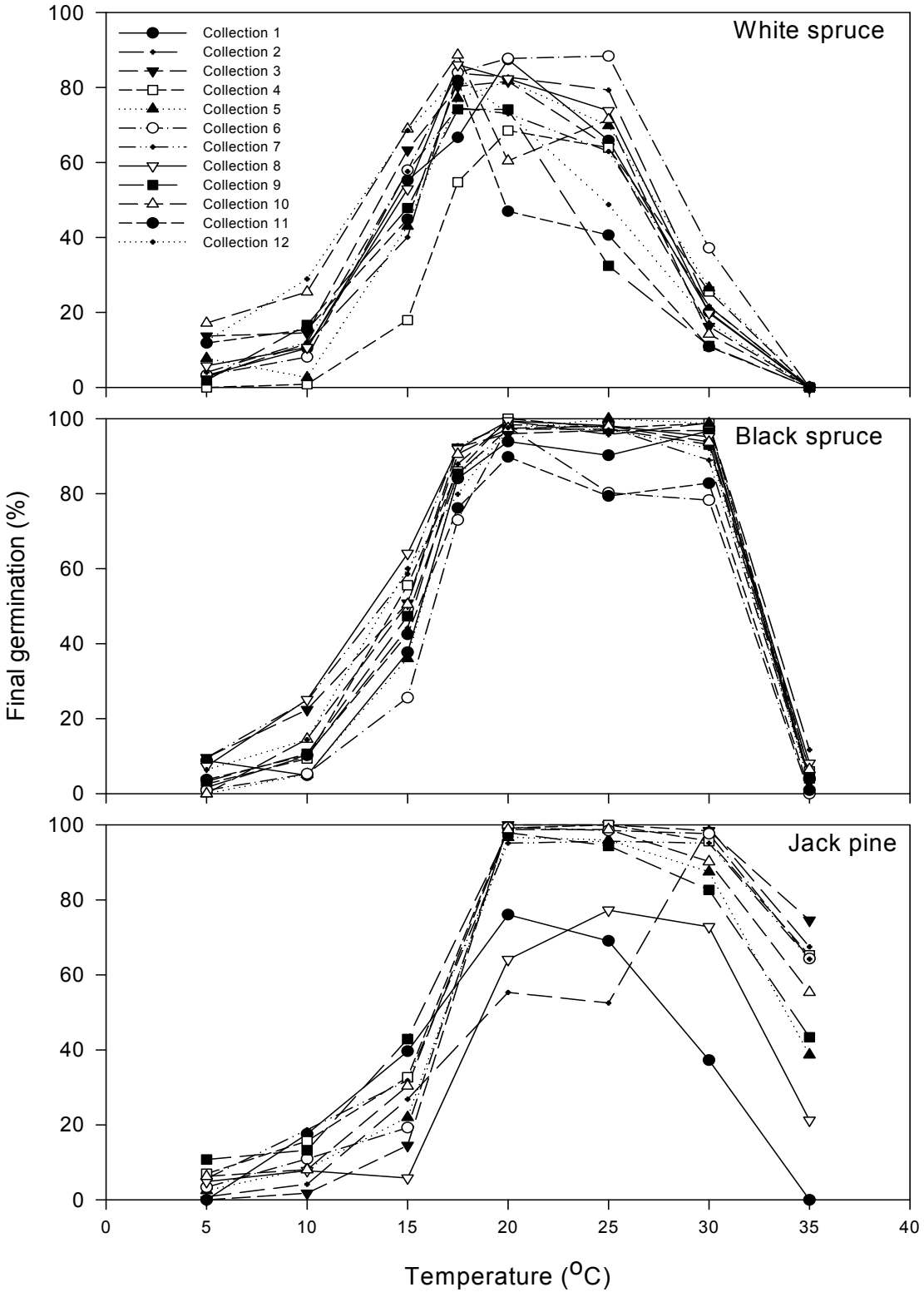

Figure 4.4. Final germination (%) for white spruce, black spruce, and jack pine collections over a range of temperatures.

4.2 Thermal time model application

4.2.1 Parameters of germination time courses from Chapman-Richard Equations

Three parameters (a, b, and c) of the Chapman-Richards Equation were obtained to describe a germination time course (Appendix C). All equations for germination time courses were significant ($P<0.001$). An adjusted R^2 value (Radj) was used to measure variance explained by the equation and taking into account the number of independent variables.

White spruce collections show the greatest variability in R^2 depending on temperature and collection (Appendix D). The smallest range of R^2 (0.80-0.97) is found at 20°C. The lowest and widest range of R^2 (0.09-0.84) occurred at 30°C. The germination time courses with the lowest R^2 were observed for Collection 4 at 17.5°C and 15°C, and Collection 11 at 25°C and 30°C. Usually when germination was low, variability in germination was high among replicates, and R^2 was low.

The majority of the black spruce germination time courses showed high R^2 (Appendix D). The 15°C temperature had the lowest germination (28%), and the largest variance in germination (28-77%) and R^2 (0.27-0.93). At higher temperatures (30°C, 25°C, 20°C, 17.5°C) R^2 ranged from 0.71-0.97. The lowest final germination percentage at high temperatures occurred in Collection 11 at 20, 30, and 35°C. Black spruce also maintained low R^2 at 17.5°C and 15°C for Collection 6, which also coincided with low germination.

High variability in R^2 was found in jack pine (Appendix D). However, high R^2 (0.69-0.95) were associated with 25°C and 20°C, when germination percentages were high (60-100%). Lower accuracy of germination time courses occurred at 35°C and 15°C. Low R^2 values coincided with low final germination percentages, specifically, no germination at 35^oC for Collection 1 and 8% germination at 15^oC in Collection 8.

4.2.2 Variation of germination in response to temperature using thermal time model parameters: T_b, $\theta_{T(50)}$, and $\sigma_{\theta T}$

The base temperature (T_b) was calculated for all collections using subpopulations, suboptimal temperatures, and germination rate (Figures 4.5-4.7). The thermal time to 50% germination ($\theta_{T(50)}$) and the standard deviation of thermal time ($\sigma_{\theta T}$) for each collection was estimated with Probit analyses (Tables 4.5-4.7). The range in average T_b was similar among the three species, but $\theta_{T(50)}$ varied among them, indicating that thermal time requirements determine the different germination rates.

In white spruce the highest overall mean $\theta_{T(50)}$ (71±7.8°C day)occurred, or the slowest germination among the three species. Collections of white spruce varied in the base temperature for germination ranging from 7.4 to 11.0°C. The base temperature for black spruce ranged from 8.1 to 11.0°C. The mean $\theta_{T(50)}$ (60±8.7°C) for black spruce collections was intermediate between white spruce and jack pine. Therefore, black spruce germinates faster than white spruce, but slower than jack pine. Jack pine collections had the broadest range of base temperatures, ranging from 3.8 to 12.5°C. Jack pine also germinate fastest with a mean $\theta_{T(50)}$ of 52±12.0°C days.

To illustrate the utility of the thermal time model, thermal time (°C day) was calculated for predicted and actual germination percentage for six collections (Figure 4.8). Both T_b and $\theta_{T(50)}$ can be used to compare seed germination response to temperature between collections or species. From these graphs the thermal time requirements of each species and collection can be compared. For example, Collection 8 of black spruce and Collection 6 of jack pine with different T_b (8.9 vs 6.7°C), but similar $\theta_{T(50)}$ (57.5 vs 55.0°C days) (Tables 4.6-4.7, Figure 4.8), indicates that thermal time requirements are similar between the two collections, but jack pine Collection 6 can accumulate more thermal time under the same temperatures because of its low T_b. T_b was

similar (8.9 vs 9.0°C) for black spruce Collection 8 and jack pine Collection 7, but the former had greater $\theta_{T(50)}$ than the latter (57.5 vs 45.7°C days), indicating that the former germinates slower.

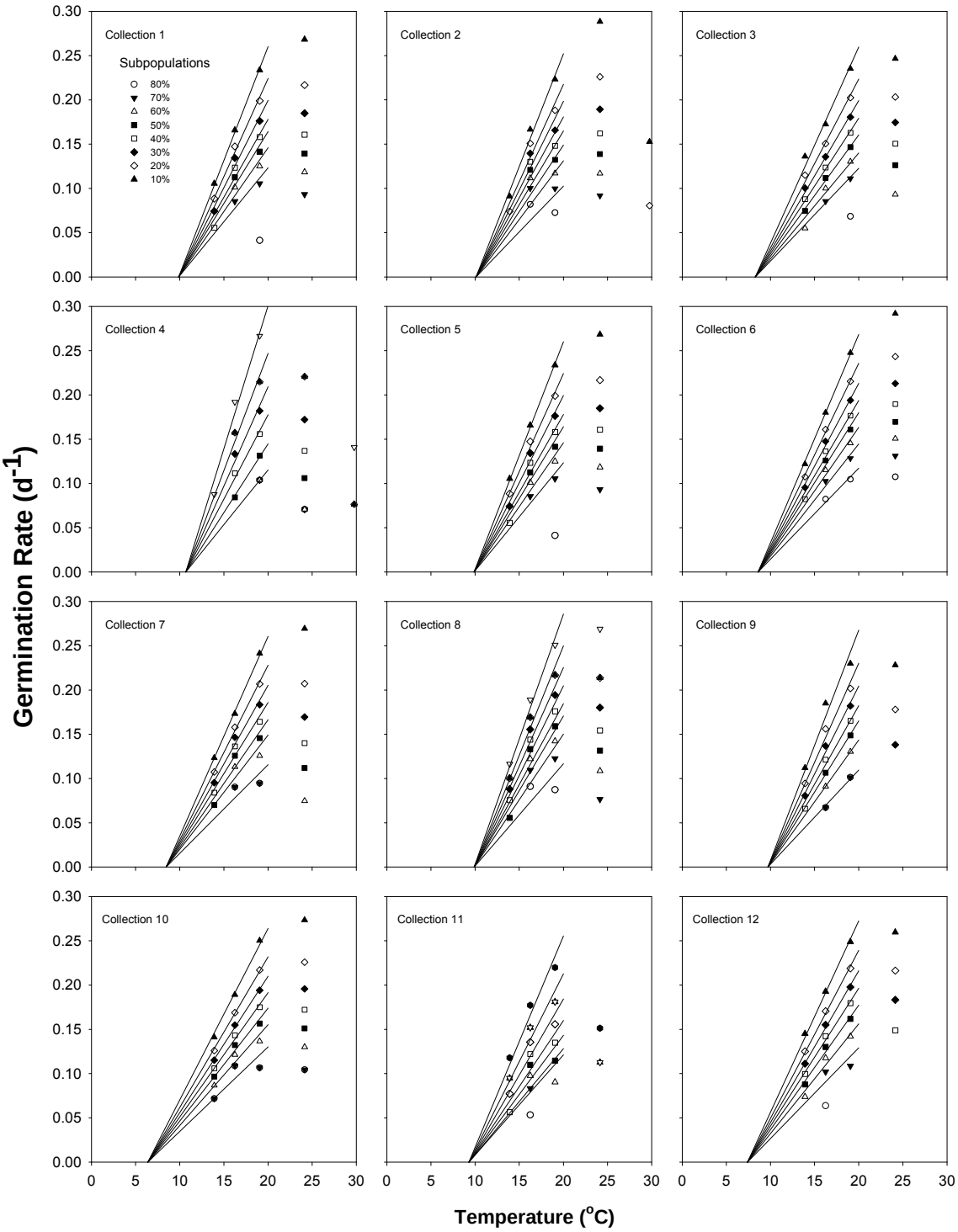

Figure 4.5. Germination rate (GR) of 12 white spruce collections within the range of sub-optimal temperatures as a function of temperature and subpopulation.

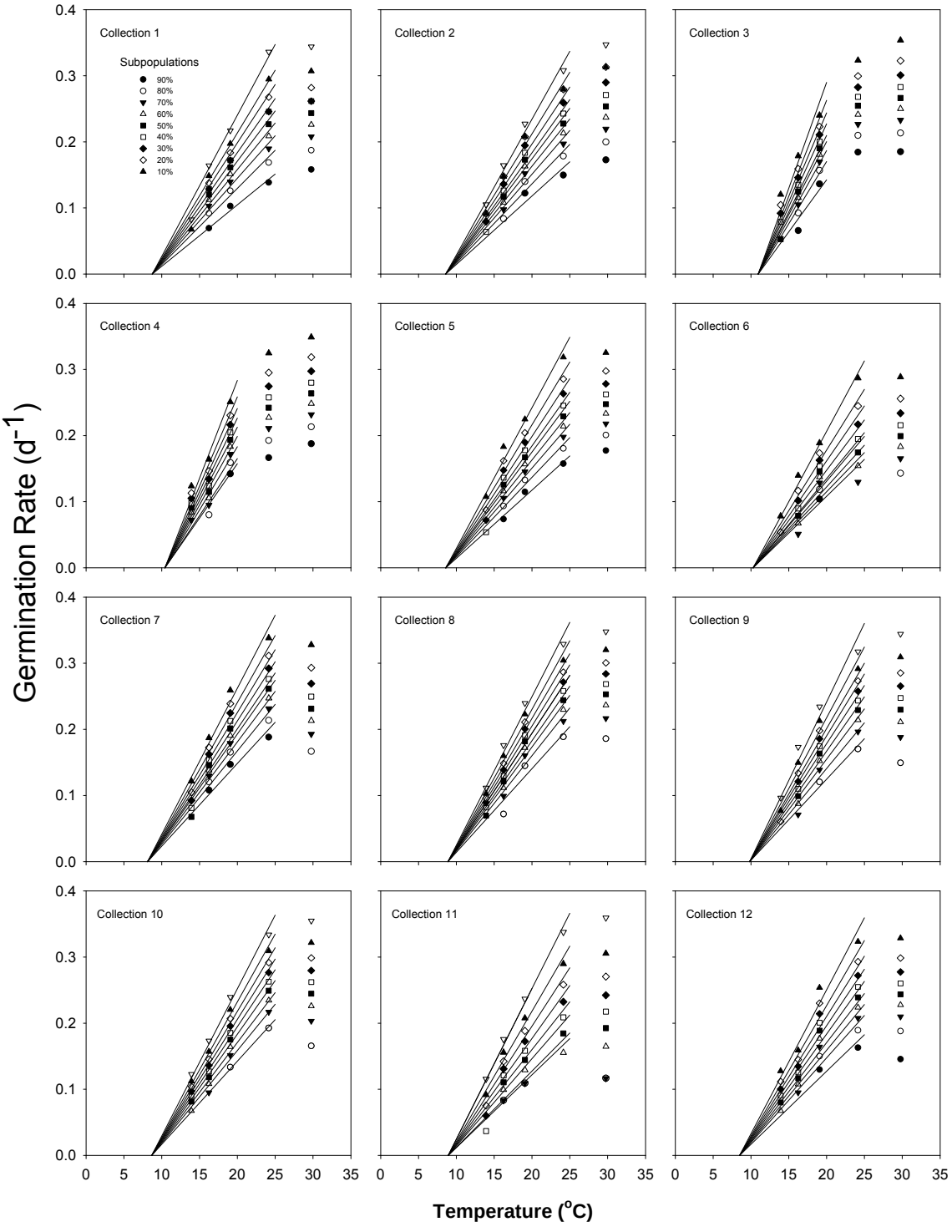

Figure 4.6. Germination rate (GR) of 12 black spruce collections within the range of sub-optimal temperatures as a function of temperature and subpopulation.

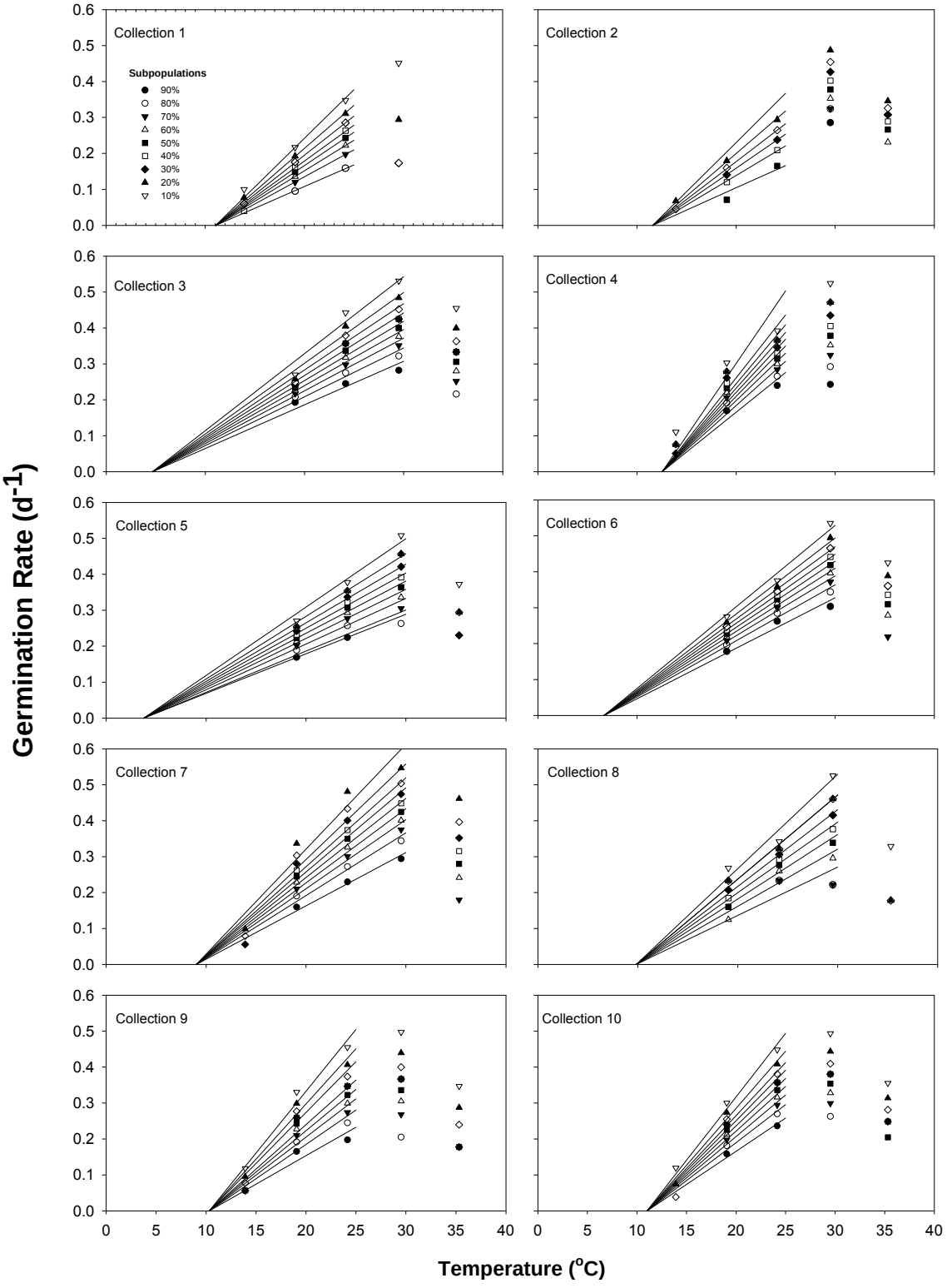

Figure 4.7. Germination rate (GR) of 10 jack pine collections within the range of sub-optimal temperatures as a function of temperature and subpopulation.

Table 4.2. Thermal time model estimated parameters for 12 white spruce collections from the Boreal Plain Ecozone in Saskatchewan. T_b=base temperature, $\theta_{T(50)}$= thermal time to 50% germination, $\sigma\text{-}_{\theta T}$= standard deviation of thermal time.

Seed Collection	T_b-(˚C)	$\theta_{T(50)}$-(˚C-day)	$\sigma\text{-}_{\theta T}$-(˚C-day)
1	9.9	74.1	2.40
2	10.1	61.7	1.51
3	8.3	79.4	1.78
4	10.7	64.6	1.91
5	9.9	74.1	2.40
6	8.6	66.1	1.48
7	8.5	72.4	1.58
8	9.9	56.2	1.51
9	9.7	66.1	1.66
10	6.4	81.3	1.48
11	9.3	75.9	1.66
12	7.4	77.6	1.70
Mean±SD	9.1±1.26	71±7.8	1.76±0.33

Table 4.3. Thermal time model estimated parameters for 12 black spruce collections from the Boreal Plain Ecozone in Saskatchewan. T_b=base temperature, $\theta_{T(50)}$= thermal time to 50% germination, $\sigma\text{-}_{\theta T}$= standard deviation of thermal time.

Seed Collection	T_b-(˚C)	$\theta_{T(50)}$-(˚C-day)	$\sigma\text{-}_{\theta T}$-(˚C-day)
1	8.8	67.6	1.38
2	8.6	66.1	1.29
3	11.0	42.7	1.32
4	10.4	45.7	1.29
5	8.6	66.1	1.32
6	10.3	69.2	1.35
7	8.1	58.9	1.23
8	8.9	57.5	1.26
9	9.8	57.5	1.29
10	8.7	58.9	1.26
11	8.9	69.2	1.45
12	8.5	63.1	1.29
Mean±SD	9.2±0.91	60±8.7	1.31±0.06

Table 4.4. Thermal time model estimated parameters for 10 jack pine collections from the Boreal Plain Ecozone in Saskatchewan. T_b=base temperature, $\theta_{T(50)}$= thermal time to 50% germination, σ-$_{\theta T}$= standard deviation of thermal time.

Seed Collection	T_b-(˚C)	$\theta_{T(50)}$-(˚C-day)	σ-$_{\theta T}$-(˚C-day)
1	11.1	56.2	1.45
2	11.6	64.6	1.70
3	4.7	61.7	1.26
4	12.5	33.9	1.26
5	3.8	69.2	1.26
6	6.7	55.0	1.20
7	9.0	45.7	1.29
8	9.8	57.5	1.45
9	10.3	40.7	1.35
10	11.0	38.0	1.29
Mean±SD	9.1±3.01	53±12.0	1.35±0.15

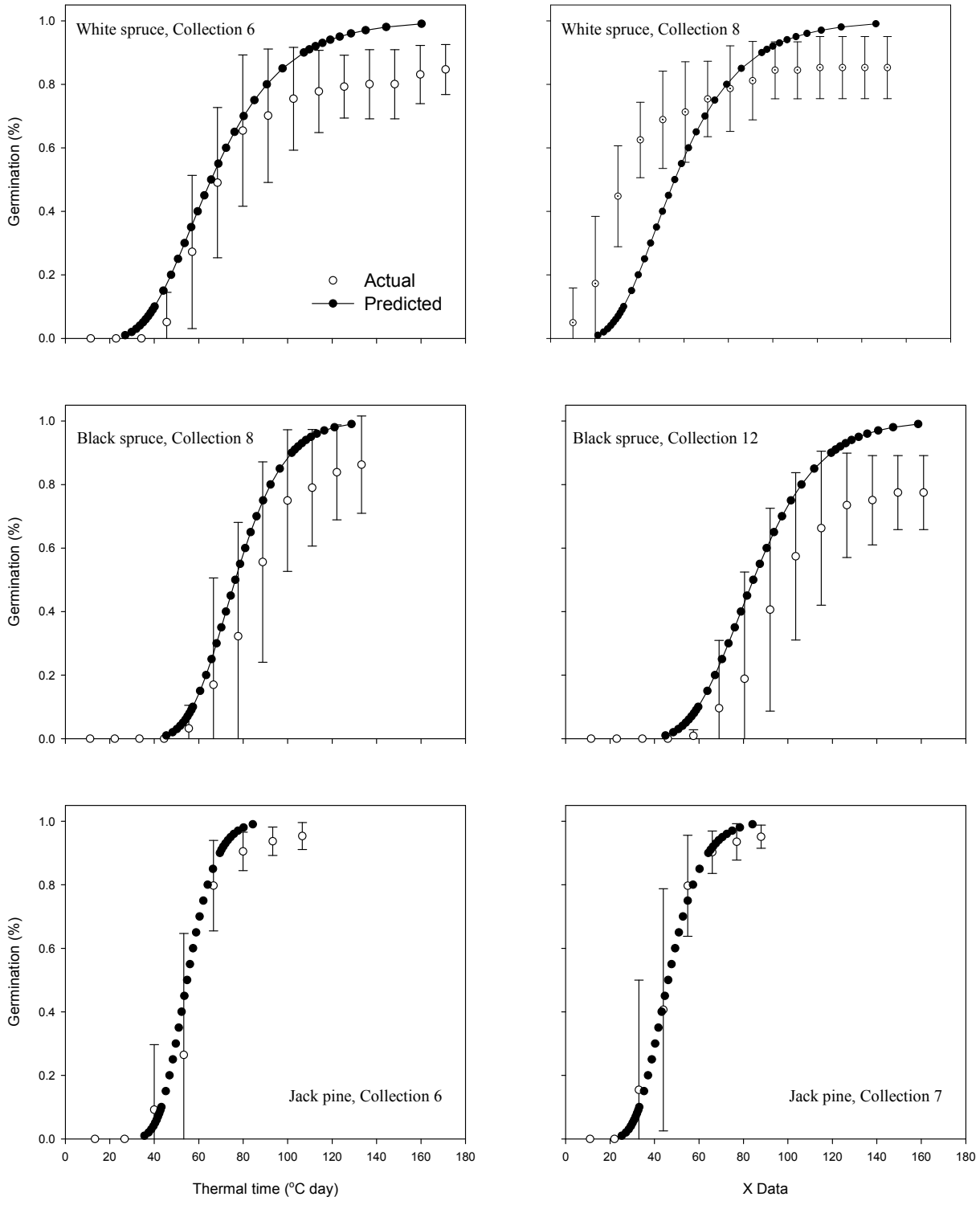

Figure 4.8. Predicted and actual germination percentages for selected white spruce, black spruce and jack pine seed collections as a function of thermal time at 20°C. Actual data are means ± SD (n=5). Predicted germination percentage was estimated using the thermal time model and associated parameters in Tables 4.6-4.8.

4.3 The impact of potential increase in spring temperatures on meeting the thermal time requirements during germination

Higher temperatures are predicted in the A2 emission scenario relative to the B2 scenario. The CGCM2 model indicates temperatures in April may rise as much as 10.3ºC by the year 2080 and May temperature may increase 11.8ºC compared to current conditions. Warmer temperatures in the spring may lead to earlier germination relative to the B2 emission scenario (Tables 4.8-4.10).

Future precipitation predicted by the CGCM2 varies by collection site and month. For white spruce, a small increase in April precipitation is often predicted. Several collection sites show an increase in April precipitation of up to 10.5 mm by the year 2080. May almost always increases in precipitation from current conditions. One exception is the site for Collection 7, where the amount of precipitation in 2080 would be similar to current amount. April precipitation patterns show little change where black spruce seeds were collected. Precipitation in May and June is predicted to increase from current conditions. One exception occurs where Collection 11 was made; precipitation is reduced under future emission scenarios. During April and May, precipitation may decrease 22.5 mm in 2020. Locations where jack pine seeds were collected show a predicted increase in precipitation throughout April, May, and June, with June having the largest increase in rainfall.

White spruce and black spruce are expected to germinate around mid-May under current temperature conditions based on T_b. Usually white spruce seeds germinate mid-May through early August (www.na.fs.fed.us). Under the high emission scenario (A2), germination will start in April by 2080. For some collection sites, advanced germination occurs a month or more earlier in spring. Under the lower emission scenario, spring germination is predicted for mid-April to early May, with the majority occurring at the end of April.

Currently, jack pine commences germination in May and continuing to mid-June. Under the predicted temperatures for the future, the timing of spring germination will advance from a few weeks to a month under A2 and B2 emission scenarios. The A2 scenario, which suggests a warmer climate in the future, predicts spring germination advancing to April for jack pine. The B2 scenario does not show a prominent advance of germination timing from current conditions, with germination starting from mid-April to mid-May.

Table 4.5 Estimated time in spring for germination to start based on the base temperature of 12 white spruce collections. Current (1961-1990) germination time is compared with future (2080) time under two emission scenarios (High emissions: A2; Low emissions: B2).

Collection #	Current	Future A2	Future B2
1	Mid-May	End-April	Early-May
2	Mid-May	Early-April	Mid-April
3	Mid-May	Mid-April	End-April
4	End-May	Mid-April	End-April
5	Mid-May	End-April	Early-May
6	Mid-May	Mid-April	End-April
7	Mid-May	Mid-April	End-April
8	Mid-May	End-April	End-April
9	Mid-May	End-April	Early-May
10	Early-May	Mid-April	Mid-April
11	Mid-May	Early-April	Mid-April
12	Mid-May	Mid-April	End-April

Table 4.6. Estimated time in spring for germination to start based on the base temperature of 12 black spruce collections. Current (1961-1990) germination time is compared with future (2080) time under two emission scenarios (High emissions: A2; Low emissions: B2).

Collection #	Current	Future A2	Future B2
1	Mid-May	End-April	Early-May
2	Mid-May	Mid-April	End-April
3	End-May	End-April	Early-May
4	End-May	End-April	Early-May
5	Mid-May	Mid-April	End-April
6	Mid-May	End-April	End-April
7	Mid-May	Mid-April	End-April
8	Mid-May	Early-April	Mid-April
9	Mid-May	Early-April	Mid-April
10	Mid-May	Mid-April	End-April
11	Mid-May	Mid-April	End-April
12	Mid-May	Mid-April	End-April

Table 4.7. Estimated time in spring for germination to start based on the base temperature of 10 jack pine collections. Current (1961-1990) germination time is compared with future (2080) time under two emission scenarios (High emissions: A2; Low emissions: B2).

Collection Site	Current	Future A2	Future B2
1	End-May	Mid-April	Early-May
2	Mid-June	Mid-April	Mid-May
3	End-April	Early-April	Mid-April
4	End-May	End-April	Early-May
5	End-April	Early-April	Mid-April
6	Early-May	Mid-April	Mid-April
7	Mid-May	End-April	End-April
8	Mid-May	End-April	Early-May
9	Mid-May	Mid-April	End-April
10	End-May	Mid-April	Early-May

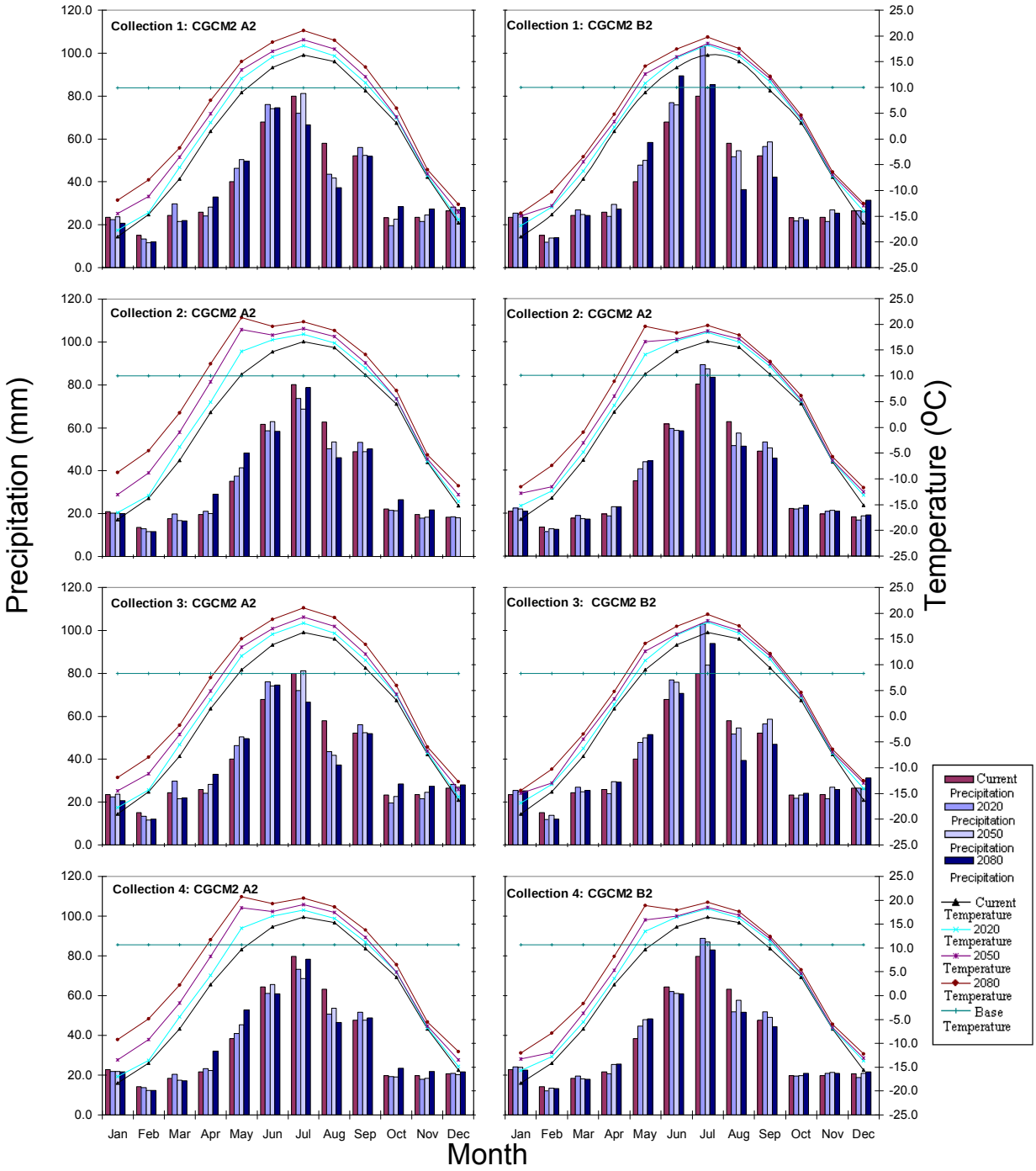

Figure 4.9. Current and predicted temperature and precipitation for 12 white spruce sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

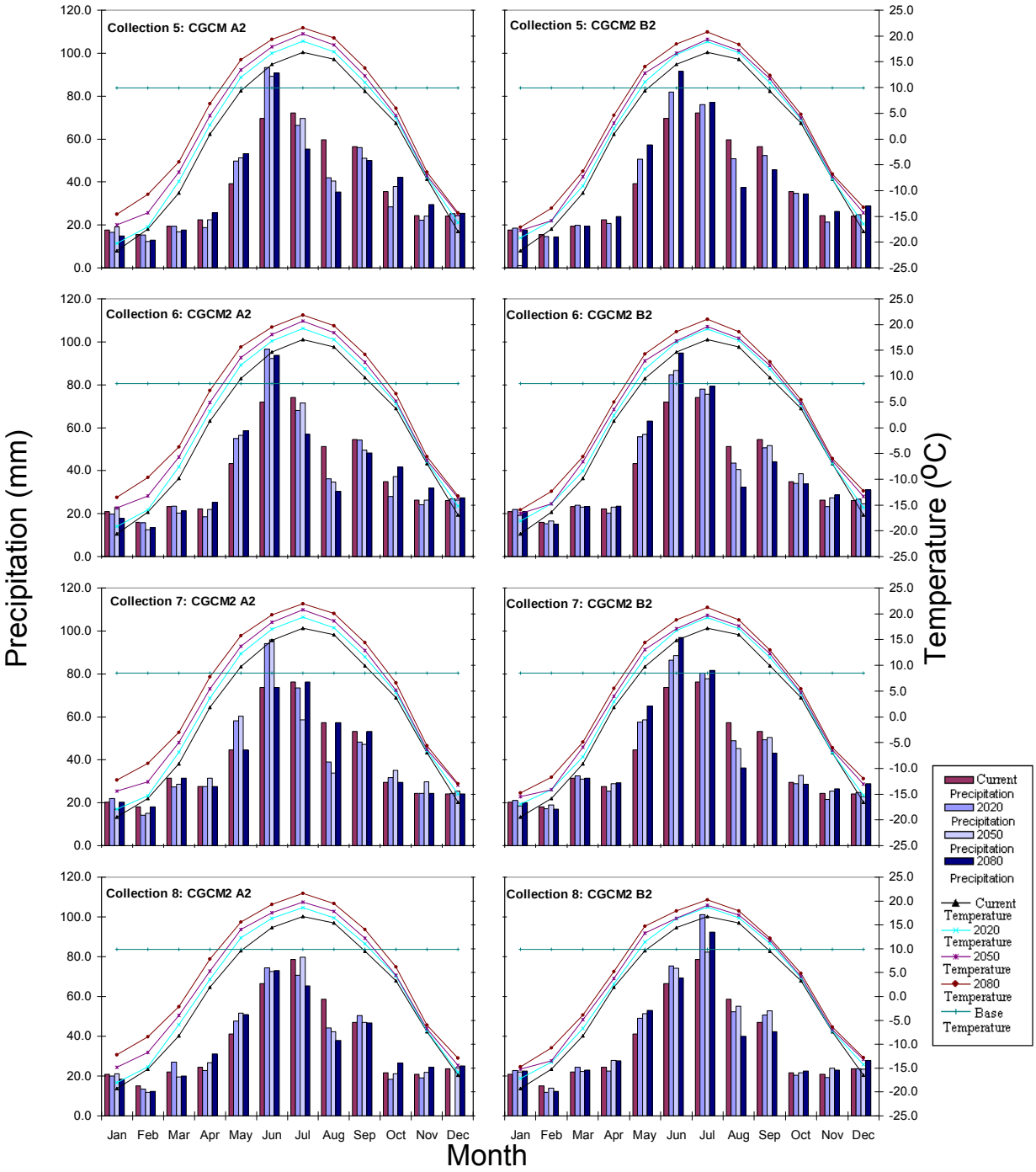

Figure 4.9 (con't). Current and predicted temperature and precipitation for 12 white spruce sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

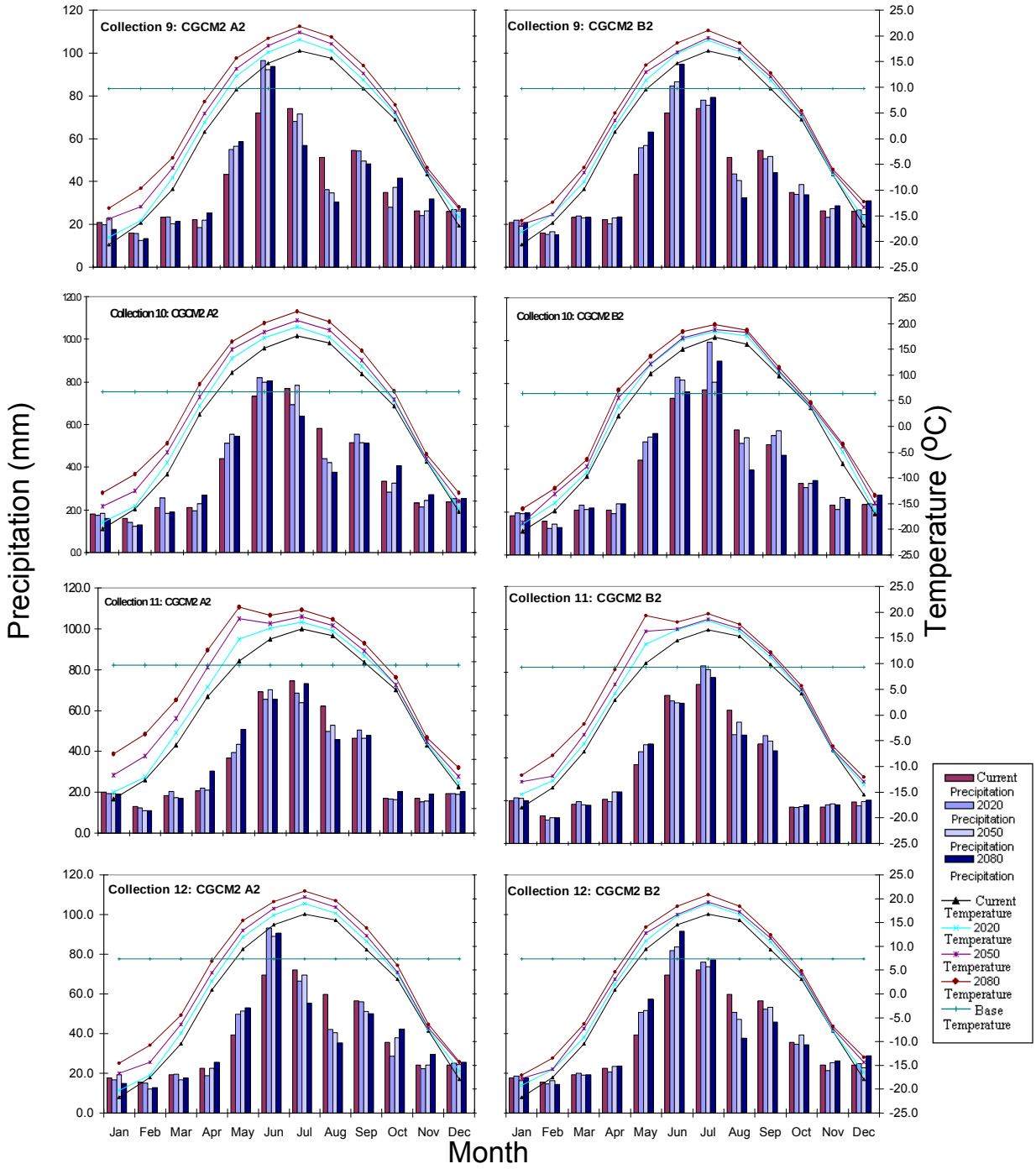

Figure 4.9 (con't). Current and predicted temperature and precipitation for 12 white spruce sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

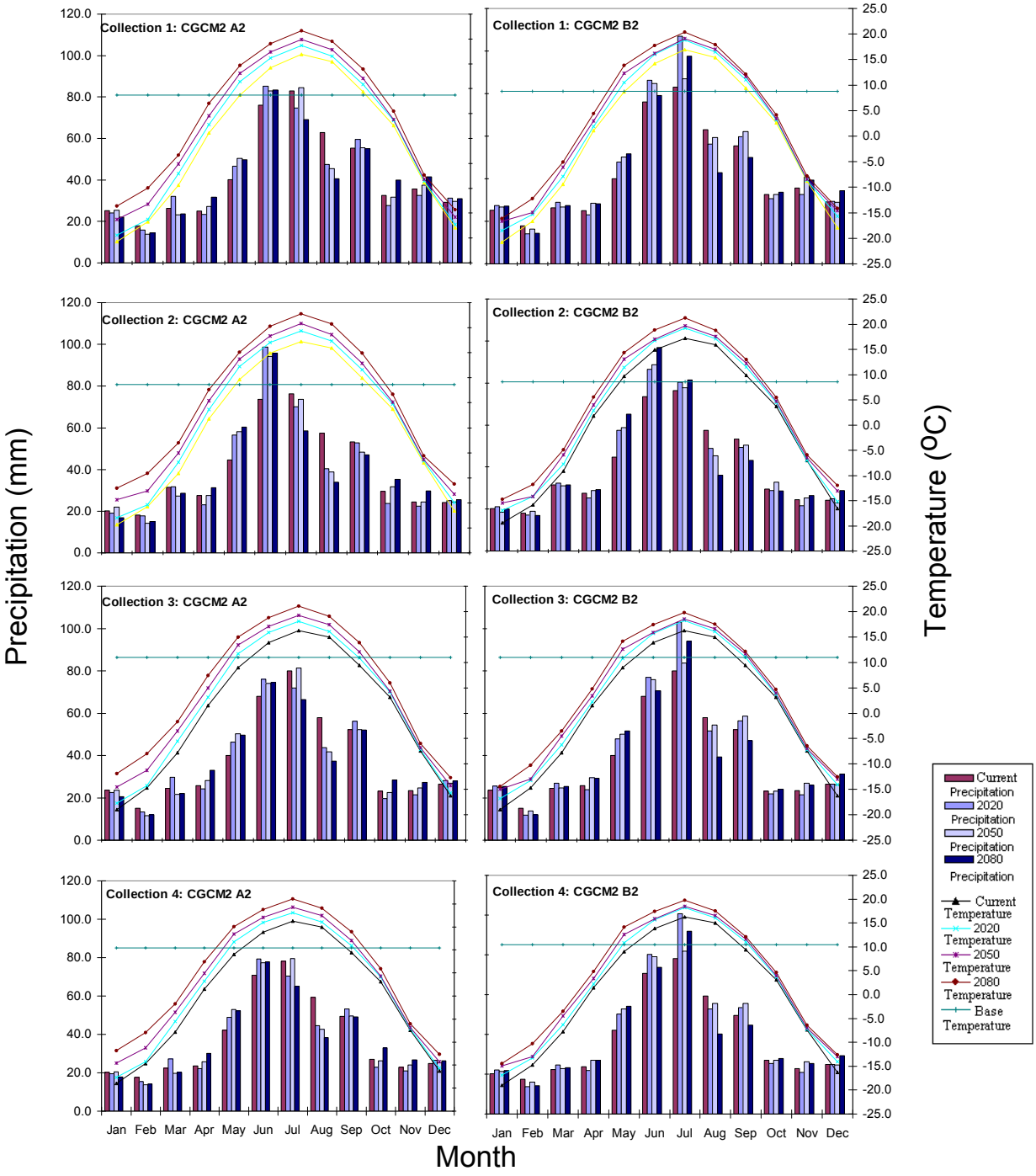

Figure 4.10. Current and predicted temperature and precipitation for 12 black spruce sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

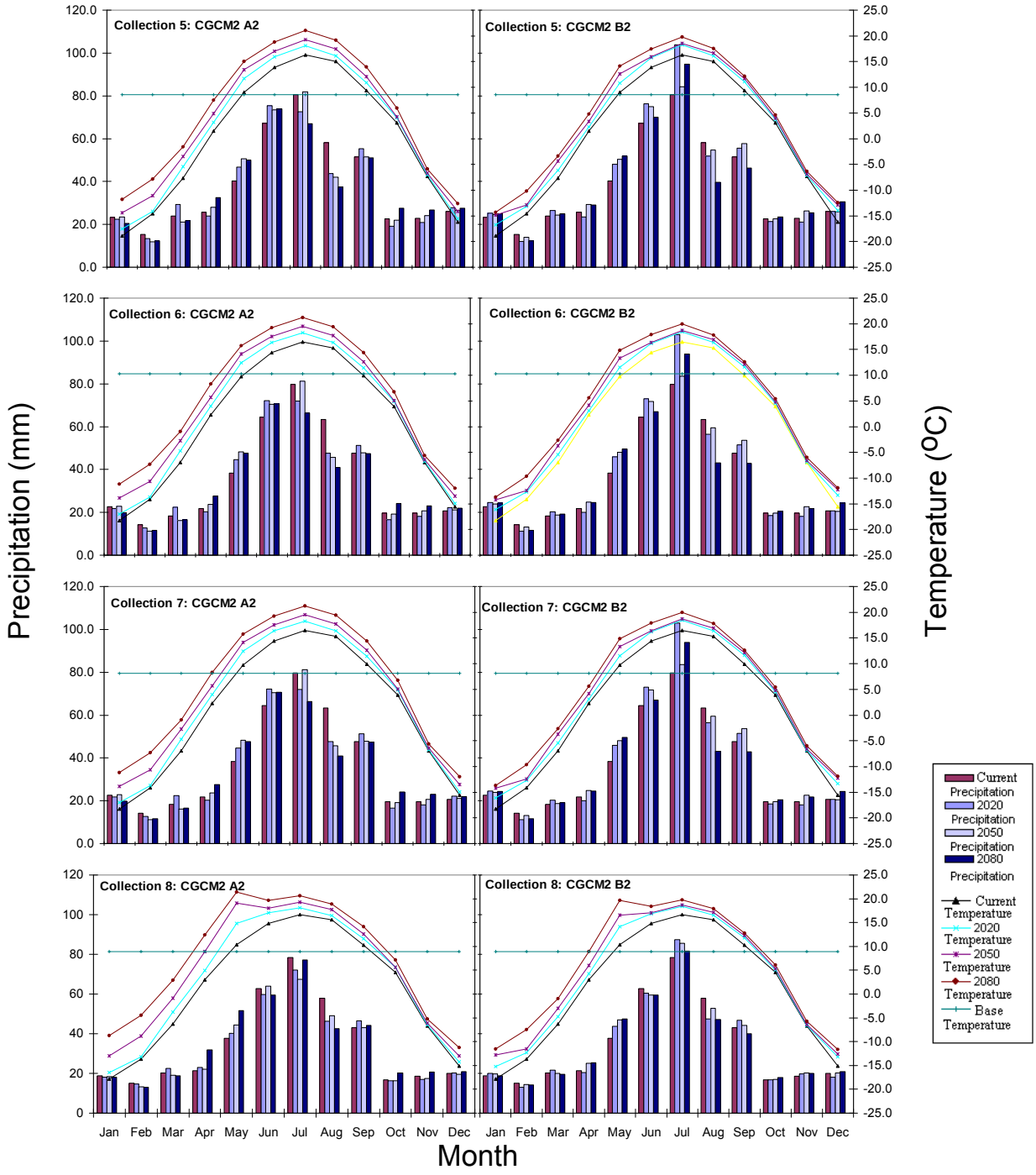

Figure 4.10 (con't). Current and predicted temperature and precipitation for 12 black spruce sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

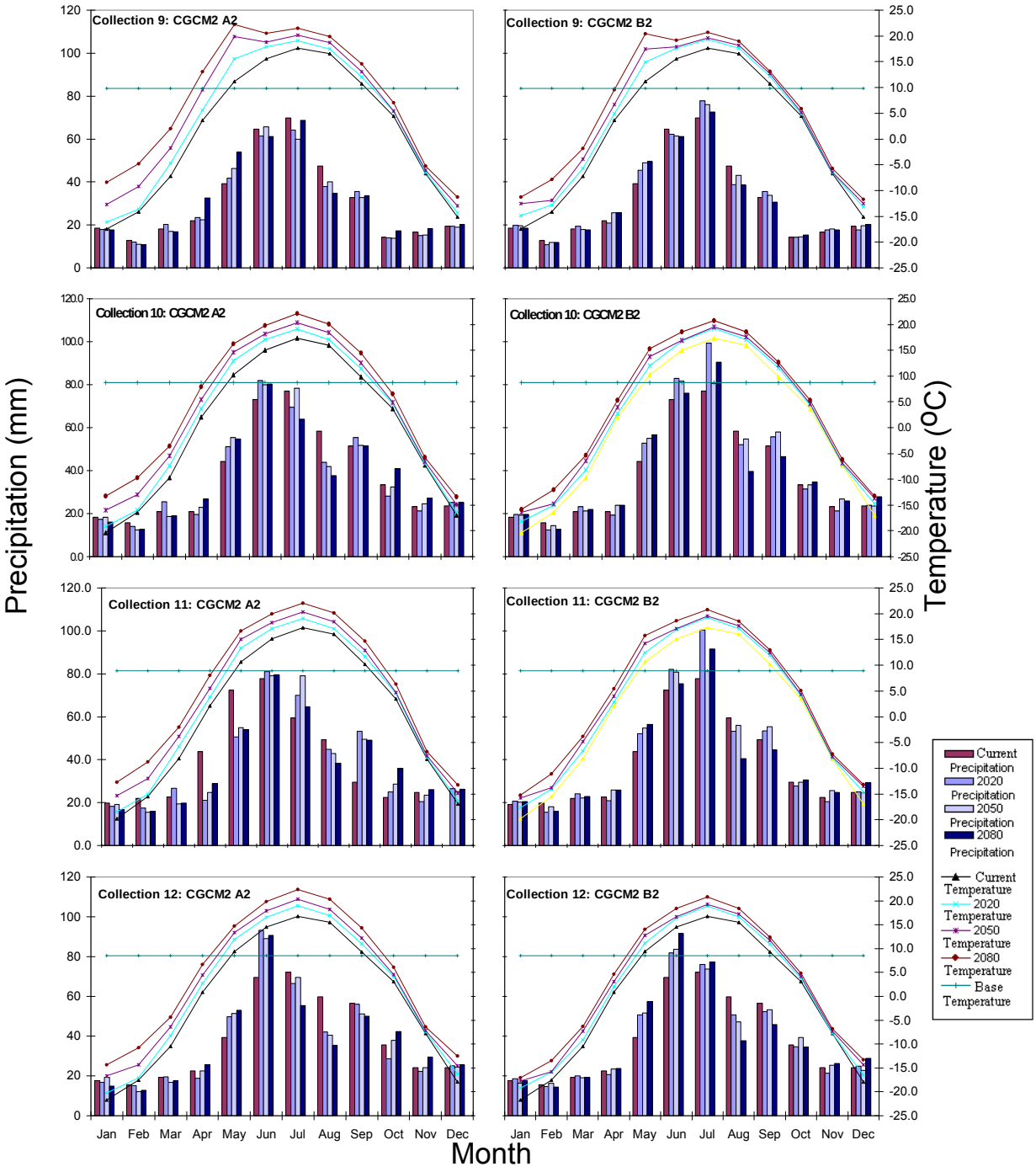

Figure 4.10 (con't). Current and predicted temperature and precipitation for 12 black spruce sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

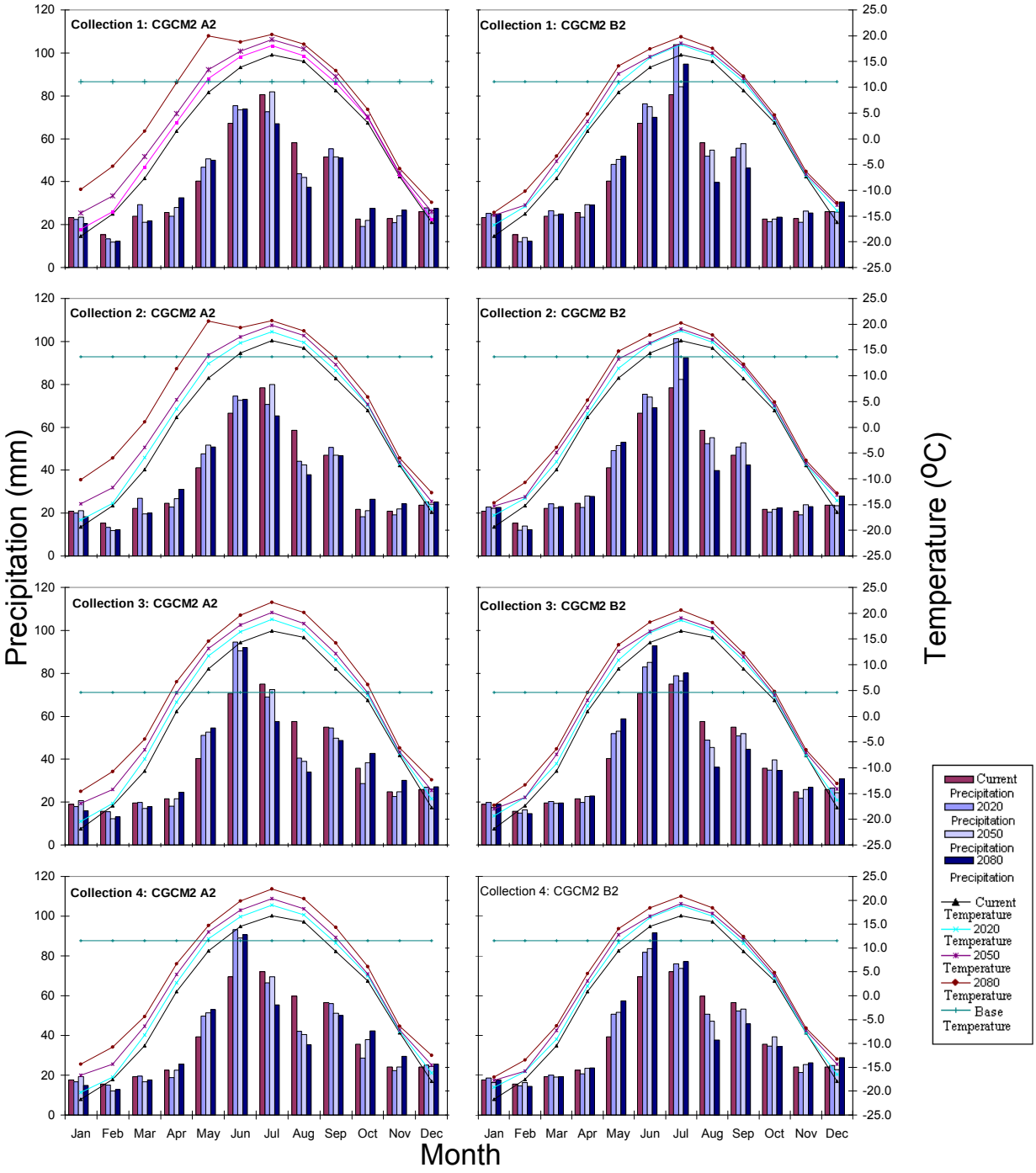

Figure 4.11. Current and predicted temperature and precipitation for 10 jack pine sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

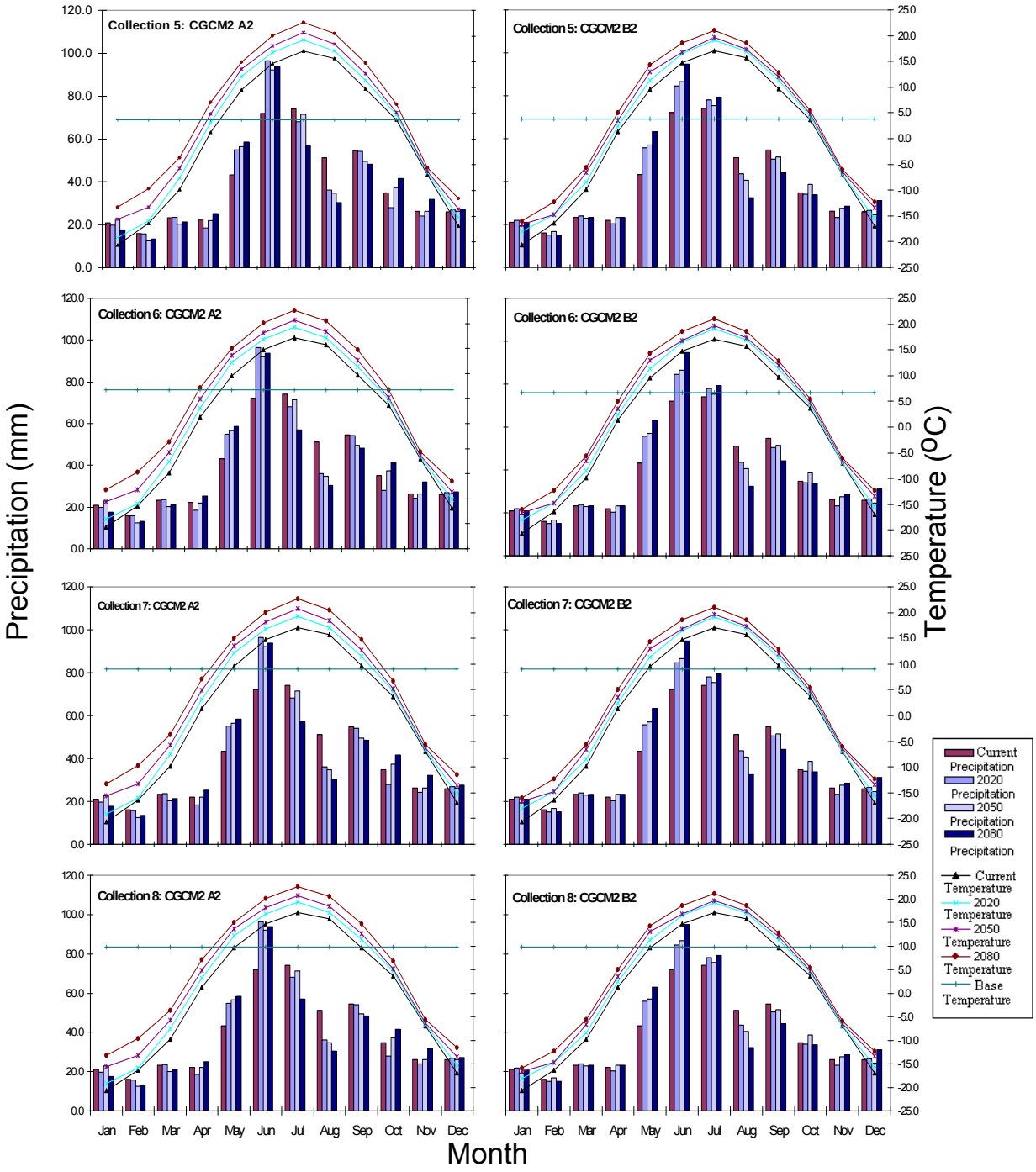

Figure 4.11 (con't). Current and predicted temperature and precipitation for 10 jack pine sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

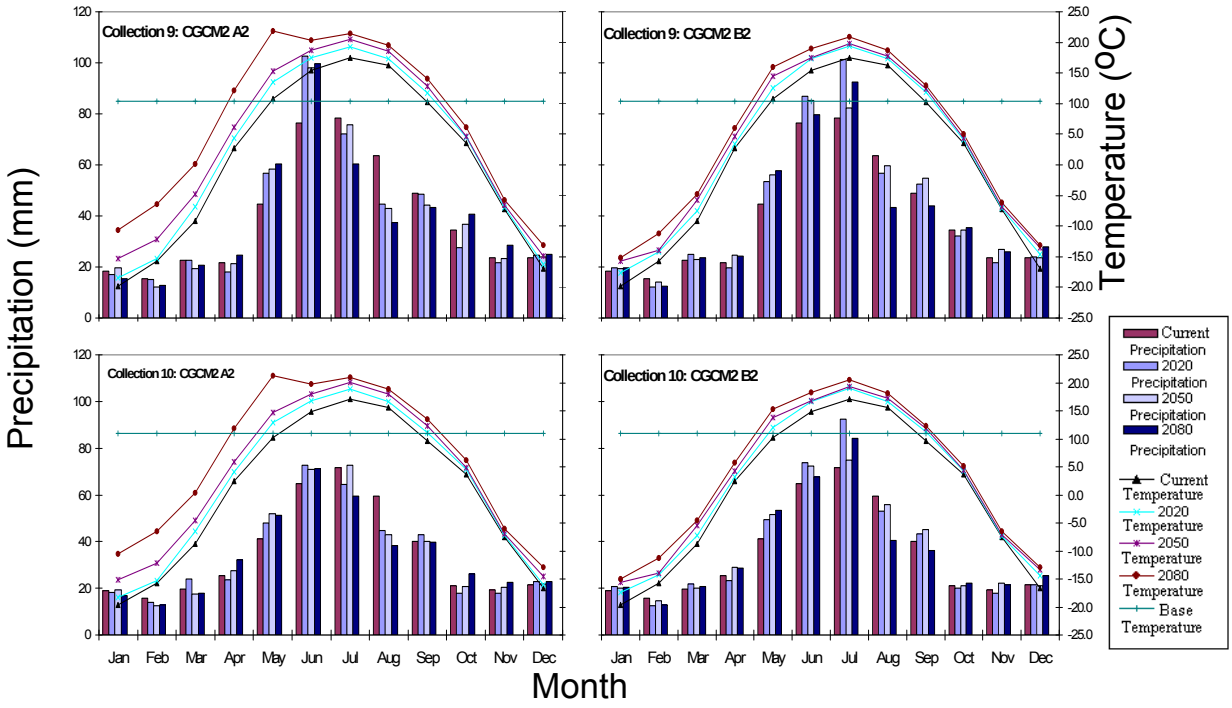

Figure 4.11 (con't). Current and predicted temperature and precipitation for 10 jack pine sites. Current temperature and precipitation (1961-1990) are compared with the Canadian Global Climate Model, version 2 (CGCM2) predicted temperatures and precipitation (2020, 2050, 2080) under two emission scenarios (High emissions: A2; Low emissions: B2). The base temperature is indicated by the horizontal line.

4.4 Linking base temperatures, $\theta_{T(50)}$ and the dormancy to geographic locations, temperature and precipitation

Among all variables analyzed, only June precipitation significantly correlated with germination parameters for white spruce (P=0.03; r=0.63) (Figures 4.12). The base temperature for the germination of white spruce increased with decreasing June precipitation. There was high P values (P=0.51-0.78) and low correlations for black spruce between environmental variables and base temperature. Therefore, differences in base temperature among collections cannot be explained by any environmental factor examined. Although all remaining regressions were not statistically significant, some trends in jack pine and its environmental parameters

emerged. For example, strong, but non-significant correlations between latitude, longitude, degree of dormancy, April precipitation, and base temperature were established for jack pine by SAS correlation analysis (Figure 4.12- 4.13). Latitude and April precipitation increased with increasing base temperature for jack pine. Therefore, more northern collection sites had higher base temperatures and precipitation. Base temperature and degree of dormancy decreased with longitude, thus base temperature and dormancy increased from east to west across Saskatchewan.

No significant correlations between $\theta_{T(50)}$ and environmental variables were found. P-values ranged from 0.11-0.68 in white spruce, 0.51-0.95 in black spruce and 0.18-0.95 in jack pine collections.

Correlations between dormancy and environmental variables were low in white spruce and black spruce. Dormancy tended to decrease from west to east in jack pine (P=0.08; r=0.58) (Figure 4.13).

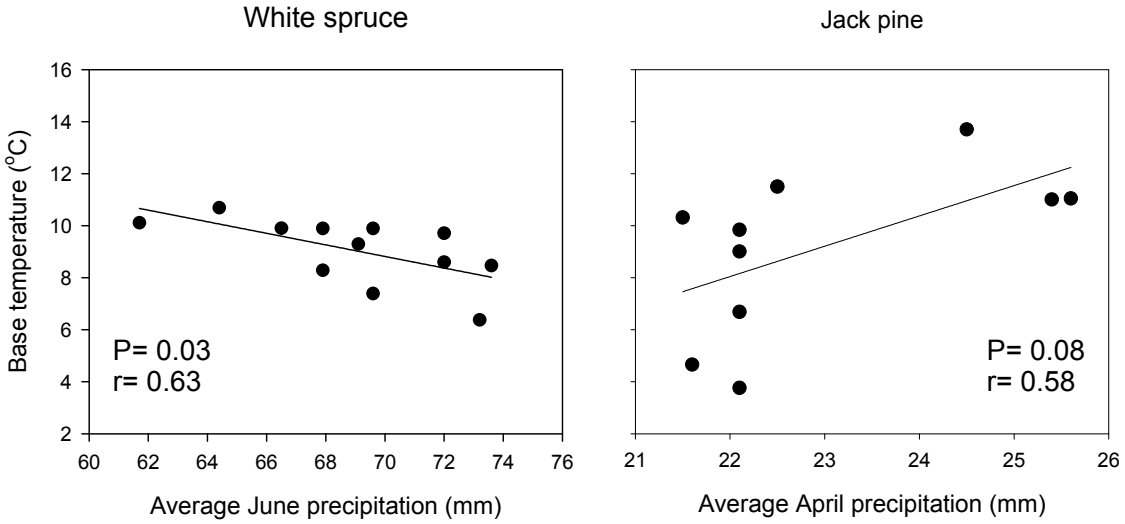

Figure 4.12. Correlations between base temperatures and precipitation for white spruce and jack pine collections.

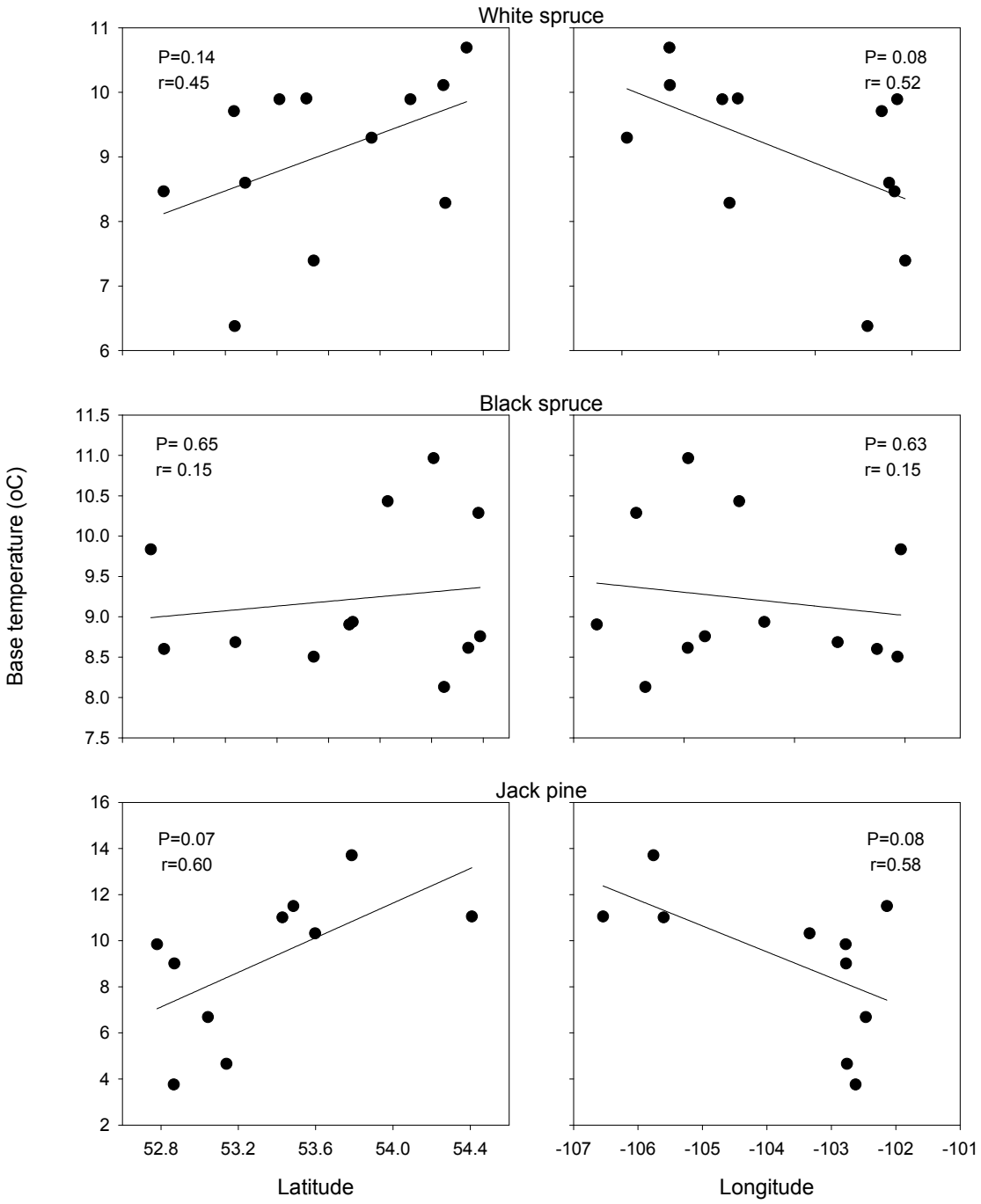

Figure 4.13. Correlations between the base temperature and latitude and longitude coordinates

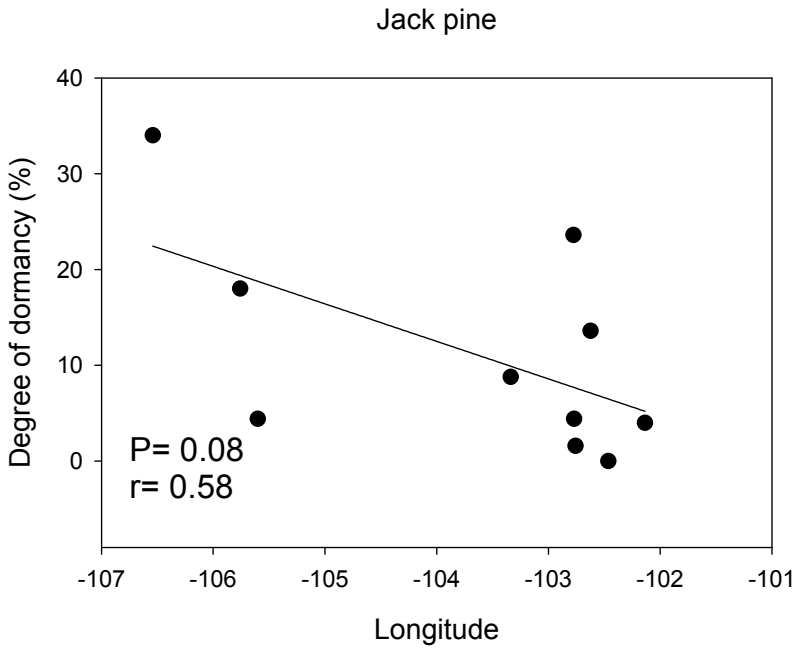

Figure 4.14. Correlation between seed dormancy and longitude for jack pine collections.

5.0 DISSCUSSION

5.1 Variation among seed collections in dormancy breaking requirements

5.1.1 White spruce

Dormancy of white spruce embryos is caused by the surrounding tissues (testa, megagametopyte and/or nucellus)(Downie and Bewley 1996). Stratifying seeds weakens these tissues, thus allowing germination (Downie and Bewley 1996). Germination of the 12 collections of white spruce showed a mixed response to stratification and light. Mixed response to stratification is in accordance with several studies on white spruce in which dormancy varies among trees, collections, years, populations, and even among seeds formed on the same tree (Caron et al. 1990; Downie et al. 1998). Downie and Bewley (1996) observed highly variable dormancy in white spruce seeds from Alberta, ranging from dormant to non-dormant depending on the origin of seeds.

Stratification may have a variety of effects on white spruce seeds. Germination of white spruce seeds from British Columbia does not respond to stratification or light (Li et al. 1994). This response was similar to Collections 4, 11, and 12 in the present study, where stratification and light had no effect on germination. Stratification increases germination in dormant seeds from Alberta, but not in non-dormant collections (Downie and Bewley 1996). In the present study, stratification improved germination in Collection 2 and 10, indicating seeds of these collections are in deeper dormancy than other collections. Collections 4, 5, 11, and 12 were unaffected by stratification, but this does not mean these seed lots are not dormant. All collections exhibited moderate dormancy (33-53%) according to viability tests. A longer

stratification period may have been more efficient in breaking dormancy in these collections as suggested by Farmer (1997). Seeds in the field are chilled for many months before germinating in the spring (Li et al. 1994). Collection 8 and 9 showed reduced germination after stratification, possibly due to seed damage during stratification.

It is acceptable and advantageous to provide light for the germination of conifers (Baldwin 1942). Light is rarely a necessity, but in most cases germination can be improved or hasten by light (Farmer 1997). Several collections of white spruce (2, 5, 8, and 10) had greater germination under light treatments. Unchilled white spruce seeds from Alaska germinated completely (90%) with a 22 h photoperiod at 15ºC (Densmore 1979). However, light does not always have a positive effect on white spruce germination. Non-stratified and stratified seeds of white spruce from British Columbia do not respond to light when incubated under alternating temperatures (Li et al. 1994). White spruce seeds from Alberta germinated equally well under light and in darkness (Downie and Bewley 1996). This response to light and darkness was similar in Collections 4, 9, 11, and 12 in this study, where light had no effect on germination. Light was not required for seed germination in four white spruce collections in this study (Collections 4, 9, 11, and 12). Some experimental evidence shows that a single, short (<1 h) exposure to light can promote germination in some seeds (Farmer 1997). White spruce seeds usually germinate in the forest understory, with little to no canopy openings (Li et al. 1994). In natural populations, white spruce is capable of regenerating under mature stands (www.na.fs.fed.us) where light may be limited, and therefore seeds have acquired the ability to germinate without light.

The effects of light and stratification on germination of white spruce seeds are poorly understood. However, stratification can alter germination response to light in loblolly pine

(*Pinus taeda* L.) and Virginia pine (*P. virginiana* Mill.) (Toole et al. 1961). Stratification altered germination in Collections 6 and 7 where only stratified seeds showed an increase in germination under light, but not in darkness. Stratification might increase seed germination in darkness, although this response was not observed in this study (McLemore 1966). Long periods of stratification may also eliminate any positive effects of light (Sterns and Olson 1958; Richardson 1959; Li et al. 1994). Thus, explaining the interactive effects stratification and light on Collections 1 and 3, where stratification had no significant effect on germination under light, but non-stratified seeds had higher germination under light. Collections 6 and 7 exhibited a different response to stratification and light. Stratification significantly increased germination under light, but light had no effect on non-stratified seeds. Reaffirming Toole et al.'s (1961) observations that stratification can alter the germination response to stratification and light in tree seeds. It is also interesting to note that Collections 6 and 7 had the lowest dormancy among all white spruce collections (27 and 28%, respectively), and these collections responded similarly to light and stratification treatments.

5.1.2 Black spruce

Black spruce germinated 70 to 100% in all collections, while stratification and light treatments had no effect on most of them. High germination was also reported in non-stratified black spruce seeds from Alaska at high temperatures in darkness (Densmore 1979).

Stratification was not required for germination of black spruce seeds in this experiment. Collections 2, 7, and 9 had reduced germination under stratification while the remaining collections were unaffected. Germination of black spruce seeds from Ontario was similar between stratification treatments (Wang and Berjak (2000). Substantial germination can occur in unchilled seeds at high temperatures in darkness or over a range of long photoperiods (>14h)

(Densmore 1979). However, black spruce seeds require long photoperiods (22h) or stratification (2-5ºC) to complete germination at low temperatures (<10ºC) (Densmore 1979). Stratification can also improve the rate and germination of non-dormant black spruce seeds at low temperatures (10-15ºC) (Farmer 1997; Wang and Berjak 2002). Farmer et al. (1984) and Densmore (1979) describe improved germination of stratified seeds at low temperatures as conditional dormancy. Conditional dormancy is likely an adaptive mechanism to prevent germination in the fall. Even though black spruce seeds are non-dormant at high temperatures, stratification might benefit seed germination if seeds are first damaged by accelerated aging (Wang and Berjak 2002). A negative effect of stratification on germination of black spruce occurred in Collections 2, 7, and 9. Light had no significant effect on black spruce germination at 25ºC. Farmer et al. (1984) indicated that the requirements for light only appear at lower temperatures in black spruce.

All black spruce seed collections had high germination and viability, indicating that there was little or no dormancy in these seed collections (0-12% dormancy). High germination is common in black spruce, especially at high temperatures (Densmore 1979; Farmer et al. 1984; Wang and Berjak 2002).

5.1.3 Jack pine

A wide variety of germination responses were observed for jack pine under stratification and light treatments. Stratification reduced germination in Collections 1, 7, and 8 under light or in darkness. Jack pine seeds have little dormancy, and germination is usually rapid (Rudoph 1982). Under natural conditions, jack pine usually releases a large amount of seeds after fire, and they can germinate quickly. Therefore, dormancy in jack pine seed does usually not exhibit dormancy as seeds usually germinates within 15 to 60 days after a fire occurrence, when there is

adequate moisture, air temperatures reaching 18° C, and continuous light; all conditions are usually found after a fire has passed through an area (www.na.fs.fed.us; Farmer 1997). At high temperatures (20-30ºC), jack pine does not require stratification (Farmer 1997), as observed in all collections in this study.

Light had mixed effects on germination of the jack pine seed collections from Saskatchewan. Germination was increased by light in only one collection (Collection 3). Continuous light at medium to high temperatures (16-27ºC) enables complete germination of jack pine (http://na.fs.fed.us). A short (<10 min) exposure to red light produces better germination relative to short photoperiods (<12 hrs) or continuous darkness at 16ºC (Ackerman and Farrar 1965); however, this effect did not occur at 21ºC. In nature, most jack pine seeds germinate following a fire when light is abundant. Therefore, light can be considered to be a natural indicator or promoter for germination following fire. Excluding light reduced germination of jack pine seeds at 15.6-26.7ºC (1982), but many collections in the present study showed different responses to light. Light decreased germination in Collection 6 in and stratified seeds in Collection 9. Collections 1, 7, and 8, however, were unaffected by light.

The interaction of light and stratification significantly affected germination in jack pine Collections 2, 4, 5, and 10. Germination of Collections 2, 4, and 5 was high under light when unstratified. High germination under light and non-stratified conditions may mimic environments after a summer fire, promoting quick germination at high temperatures. Stratified seeds of these same collections, germinated equally well under light and in darkness at the same temperature whereas light reduced germination in Collections 2, 5, and 10 after stratification. Reduced germination under light may be a mechanism preventing jack pine seeds from germinating in the forest understory until spring. Unlike other collections, Collection 10 had

significantly higher germination under light than in darkness after stratification. This collection may germinate in the spring as opposed to germinating immediately after a fire.

Jack pine had the largest variation in seed viability (73-99%) and dormancy (0-34%) among all three species. When incubated at high temperatures, jack pine has high germination (Farmer 1997), which is comparable to the viability and germination observed in this study.

5.2 Response of different seed collections to temperature during germination

5.2.1 White spruce

The minimum constant temperature reported for germination 5°C, and few seeds germinate below 10°C in white spruce (http://na.fs.fed.us). Fraser (1971) estimated that the lowest temperature for white spruce germination ranged from 7.2°C to 10°C. However, no attempt has been made to determine the germination threshold of conifers. Among the white spruce collections studied, the mean base temperature was 9.1°C. High base temperatures (10.1 and 10.7°C, respectively) and low germination at 15°C occurred in Collections 2 and 4, which were from northern locations. Therefore, Collections 2 and 4 may have adapted to cooler temperatures and require warmer temperature for germination. This mechanism prevents early germination of seeds in a harsher climate. By contrast Collection 10, from the southern Boreal Transition Ecoregion had the lowest base temperature (6.4°C), greater germination at lower temperatures, and produced the highest final germination and lowest variability among replicates. Variation between replicates became increasingly large as temperature increased within the supra-optimal temperature range (25-35°C) and germination at 35°C was limited. Germination of several white spruce collections from across Canada was also inhibited at 32.2-37.8°C (Fraser 1971). Maximum temperatures for white spruce germination are between 29°C

and 35°C (Densmore 1979). At these temperatures, germination rate and percentage of white spruce seeds were reduced (Fraser 1971). In Collection 6 the highest germination at 25 and 30°C were found, this collection may be favored by climate change. Lower germination at higher temperatures in Collections 10, 11 and 12 may show reduced germination under global warming.

Optimal germination for white spruce occurred at 20°C, as indicated by the linear relationship between germination rate (GR) and temperature. This concurs with Fraser (1971), wherein an optimal temperature range was 12.8°C to 23.9°C for white spruce collections across Canada. The collections of white spruce in the present study were from the Mixed Wood Section of Saskatchewan, which may not be a large enough geographic distance to produce large differences in optimal germination temperatures.

No previous studies have investigated the thermal time requirements for the germination of conifers. The average $\theta_{T(50)}$ of 71°Cd^{-1} for collections of white spruce in Saskatchewan was higher than black spruce and jack pine. Given similar germination temperatures, white spruce requires more thermal time and seeds germinate slower germination than the other two species.

5.2.2 Black spruce

Similar to white spruce, low germination at low temperatures occurred in black spruce, which could have been caused by conditional dormancy (Densmore 1979; Farmer et al. 1984). Under natural conditions, this type of dormancy would prevent fall-dispersed seed from germinating (Farmer et al. 1984). However, most black spruce seeds are usually released in the spring due to cone serotiny, and conditional dormancy as a prevention mechanism is no longer needed. Therefore, conditional dormancy in black spruce may have been developed in an earlier period before the development of cone serotiny (Farmer et al. 1984). Collection 1 is a northern

collection with the lowest germination; this low germination indicates conditionally dormant seeds exist in this collection.

The optimal temperature for black spruce germination was between 20°C and 25°C. The base temperature for black spruce germination was between 5°C and 15°C. There were no correlations among collections of black spruce thermal time parameter and geographic locations. The average thermal time requirement for 50% germination was 60°C d^{-1}. Overall, black spruce seeds germinated faster than white spruce, requiring less thermal time to reach 50% germination. Collections 3 and 4 had the lowest $\theta_{T(50)}$ (43°C d^{-1} and 46°C d^{-1}, respectively), and thus they have potential to accumulate heat faster and germinate faster than other collections even though their base temperatures were slightly higher. Genetic variability in black spruce occurs along a north to south geographic gradient (http://na.fs.fed.us) and different ecotypes related to upland and peat land sites have been reported (Morgenstern 1978). The geographic range of the collections in the present study may not be large enough to reveal spatial patterns in germination even though variation in germination existed among collections.

5.2.3 Jack pine

Low germination occurred at low temperatures in jack pine. Collection 1, the most northern collection site showed higher germination at 15°C relative to other collections. Many studies have shown that seeds from northern sources often germinate at lower temperatures relative to southern seed sources (Fraser 1971). Collections 5 and 8 were located in the southeast region of the study area, and exhibited the lowest germination at 15°C (<20% germination). At 20°C to 30°C, jack pine showed high and fast germination as reported earlier (Ackerman and Farrar 1965; Rudolf 1965; Farmer 1997).

The optimal temperature for jack pine varied among collections. Collections 3, 5, 6, 7, and 8 are located at the southern part of the study area, and the optimal temperature for germination was 30°C and revealed lower base temperatures than other collections (<10°C). By comparison, the remaining collections from the northern part of the study area (1, 2, 4, 9, and 10) with an optimal temperature of 25°C and base temperatures above 10°C, showed different temperature requirements based on grouping of collections.

The average base temperature for jack pine collections was 9.0±3.01°C d^{-1}, similar to that of white spruce and black spruce. The highest variation in base temperature among the three species occurred in jack pine, ranging from 3.8-12.5°C (Collections 5 and 4, respectively). In jack pine the smallest thermal time to 50% germination was 34°C d^{-1} and the highest base temperature (12.5°C) occurred in Collection 4. Collection 5 had the lowest base temperature (3.8°C), but the highest thermal time to 50% germination (69°C d^{-1}). Jack pine is known to be highly variable in climatic adaptation, growth and form, and can exhibits large genetic diversity (Rudolp 1982). Fast germination is important in jack pine because it usually germinates following fire (Rudolph and Yeatman 1982) when competition with other species is low (Cayford et al. 1967).

5.3 Spatial variation in germination according to geographic locations, temperature, precipitation and degree of dormancy

At global or continental scales, climate is the primary force governing the distribution of vegetation (Retuerto and Carballeira 2002). Genetic variation is often associated with the origin and adaptation to local conditions (Carter 1996). If the range of environmental conditions is large enough, variation associated with location or source of seeds canoccur in tree species (Mergen 1963). Most forest tree species show genetic variation at the regional scale in response

to changing environmental conditions (Morgenstern 1996). Variation can be clinal (gradual transitions paralleling environmental change) or ecotypic (Mergen 1963).

5.3.1 White spruce

Among the variables examined in this study, the base temperature of white spruce was significantly correlated with average June precipitation, where the base temperature decreased with increasing precipitation. The optimal temperature for germination of white spruce was 20°C, a temperature that can occur in June. Therefore, June precipitation is critical for successful germination. Although the base temperature for germination is reached in May, germination temperatures are low and most seeds cannot germinate. For the growth of white spruce, local adaptation to temperature, but not moisture conditions, is important (Andalo et al. 2005). The present study has shown that germination of different white spruce collections varies across the range of the Boreal Plain Ecozone of Saskatchewan in relation to temperature and June precipitation. Other studies have proven spatial variation in white spruce can follow north to south trends in seed weight, germination capacity, hypocotyl length and four-month seedling height (Khalil 1985). East to west trends in white spruce includes seed weight, cotyledon numbers, and four-month seedling height (Khalil 1985). Nienstaedt and Teich (1972) described the spatial pattern in white spruce as clinal, following latitudinal and altitudinal gradients. This shows that white spruce is adapted to diverse climate and edaphic conditions across North America (Lesser et al. 2004). Although this study did not demonstrate spatial variability in temperature, degree of dormancy or other germination parameters, white spruce can still be considered as a tree with spatial variation adapted to many other characteristics. This study may not have covered a large enough geographical distance in order to discover spatial variation in germination requirements.

5.3.2 Black spruce

Black spruce germination did not show any correlate significantly with environmental variables examined. Other studies across a larger geographical range have shown some spatial variation exists in black spruce. For example, the boreal forest and forest-tundra of eastern Canada has been significantly correlated with their thermal sum (number DD >5°C) along the latitudinal gradient (Meunier et al.2007). Spatial variation in germination was found by Meunier et al. (2007) where decreased seed germination occurred from 53°N to 58°N. Therefore, the Boreal Plain Ecozone of Saskatchewan may not be a large enough study zone to produce variation in seed germination of black spruce.

5.3.3 Jack pine

There was a weak correlation between base temperature and average April precipitation in jack pine collections. Therefore, April precipitation is critical to jack pine germination. Opposite of white spruce, base temperature increased with increasing precipitation in April. Studies on growth of jack pine indicate that this species has a clinal pattern of growth associated with latitude (photoperiod) and the length and temperature of growing season of seed sources (Rudolph and Yeatman 1982). Seed yield was not correlated with latitude and longitude of seed sources (Rudolph and Ceich 1979). However, germination differed significantly among 15 provenances of jack pine, and appeared to be related to site quality but not longitude (Rudolph and Yeatman 1982). Site quality or habitat type seems to be a better factor in determining different characteristics of germination. The degree of dormancy increased from east to west across Saskatchewan in the present study, although it was not significant.

5.4 General discussion and implications

The warming in the boreal forest by the end of this century is expected to be greater than that in the last 10,000 years (Stewart et al. 1998), causing a northern shift of the boreal forest zone and a replacement in the southern boreal regions by grasslands (Sargent 1988; Rizzo and Wiken 1992; Hogg 1994). The Canadian Global Climate Model version 2 (CGCM2) predicts a greater increase in spring and summer temperatures than fall or winter, with April and May temperature rising as much as 10.3°C and 11.8°C, respectively, from current temperature conditions at some locations. This temperature increase may have large implications for the timing of seed germination in the spring. Using base temperature as a guideline, germination temperatures may be reached by up to a month earlier in the season.

White spruce seeds are dispersed in August through September and they germinate in field conditions from mid-May through early August when soil surface temperatures are warm (http://na.fs.fed.us). Germination is usually complete by early July (Hellum 1972). Black spruce trees disperse seeds over several years, but within years, most dispersal occurs in the spring (http://na.fs.fed.us). The base temperature for germination of black spruce seeds can be reached in mid-May under current conditions. Jack pine seeds are released following fire and most seeds germinate in the first or second season following a fire (http://na.fs.fed.us). By 2080, the base temperature for germination will be reached in April for most collections due to climatic warming. However, germination may not occur at this early in the season because water may be a limiting factor under future climatic conditions. Even though, the amount of precipitation increases under climate change scenarios, the amount of future precipitation in April does not equal the current May precipitation amounts, and higher temperatures may lead to greater evaporation. Therefore, water may be a constraint against early germination of these species.

The timing and capacity of germination is important for regeneration and perpetuation of conifers, especially under global warming. The most critical period during the life cycle of conifers is the first few weeks of seedling development (Daniel et al. 1979). Hogg (1994) postulated that moisture limitations do not allow conifer regeneration south of the present limit of distribution because this limit corresponds closely with climatic moisture regimes (Annual precipitation – Potential evaporation). White spruce, black spruce and jack pine grow in much warmer regions of eastern North America where water is not limited so temperature is not the limiting factor on conifer distribution in its southern boundary. If the current southern limit of boreal species is climatically restricted by lack of water available to seed establishment, a small shift to drier conditions in this region could have a significant effect on natural conifer regeneration and distribution of these species (Hogg 1994).

Species and ecotypes can respond to temperature changes differently. Tree species have migrated independent of each other in the past, and they continue to expand and contract their natural ranges as individuals respond to varying environmental conditions (Davis 1983). Species or ecotypes with a wide range of temperature or environmental tolerances (broader ecological niches) will have a greater ability to adapt to climate change, especially species favored by warmer temperatures.

White spruce has a lower optimal temperature for germination than black spruce and jack pine and high temperatures reduced germination especially in Collections 9, 10, 11, and 12. Collection 6 showed the highest final germination under high temperatures (20-30°C) among all white spruce collections. This collection may be the best suited for germination under warmer temperatures caused by climate change. However, none of the white spruce collections germinate as well as black spruce or jack pine under the same high temperatures. Therefore,

white spruce may have a reduced ability to germination under climate change and increasing temperatures relative to black spruce or jack pine.

Most black spruce collections have poor germination at 15°C and lower, and high germination at 15-30°C (<90%). This species does not show large variation in germination among collections, although optimal temperatures for germination varied from 20 to 25°C. Therefore, black spruce may be better adapted to higher temperatures provided moisture is not limiting. Poorer germination occurred at 20-30°C in Collections 1, 6, and 11, relative to other collections. These collections may be the most ill suited for germination under global warming relative to other black spruce collections.

A broader temperature range occurred for jack pine germination relative to white spruce or black spruce. Seeds germinated between 5 to 35°C in most collections and reached 75% at 35°C (Collection 3). Neither white spruce nor black spruce are able to germinate at this temperature. Jack pine may be most suited to survive under climate change. Collections 1 and 8 are two collections that may have reduced germination under a warmer climate, they require lower temperatures, and have reduced germination at higher temperatures relative to other collections.

Species around the world are shifting their distribution towards higher altitudes and latitudes to keep up with global warming (Fox 2007). This rate of warming may be too fast for some species to migrate (especially trees which have a long life cycle), as optimal temperature conditions may shift hundreds of kilometers closer to the poles. Conservation biologists have been discussing assisted migration as a method for dealing with the forecasted effects of global warming on biological species. This study can be used to identify certain seed sources that may be candidates for assisted migration under climate change. For example, white spruce seed

collections that favor warmer temperatures may be a viable seed option for planting in more northern regions in preparation for climate change.

5.5 Conclusion

Germination varied among seed collections in white spruce, black spruce, and jack pine germination in the Boreal Plain Ecozone of Saskatchewan. Some collections may germinate poorly under a warmer climate, decreasing their regeneration potential. However, a few collections have an affinity towards germinating under warmer germination, and they may have the ability to flourish under warmer climates given adequate moisture. Climate change may lead to a replacement of species or populations of species that require colder temperatures for germination by species or populations that favor warmer germinating temperatures. As Stewart et al. (1998) predicted, over the next 50-100 years, the geographic range of species in the boreal forest might shift 300-500 km north because of changing climate.

Predicted temperatures using the CGCM2 climatic model indicate germination could begin up to a month earlier as temperatures suitable for germination will be reached earlier in the season. However, if climate shifts towards higher temperatures and drier conditions, many ecotypes will become restricted to moister areas and this limitation may cause a shift northward in conifer distribution where moisture may be more abundant. The current limit of the southern boreal forest is set by the climatic moisture regime and therefore may be the most important factor under climate change (Hogg 1994). Future studies expanding on this area of research could investigate the interaction of moisture and temperature on these species using a hydrothermal time model. This model would allow more accurate predictions of germination of these species in relation to moisture. Other environmental factors such as insects, fire intervals, diseases, plant migration rates, species interactions, and competition must also be considered.

The uncertainty of climatic models combined with this wide variety of variables creates difficulty in predicting the exact fate of the boreal forest and distribution of individual species under climate change. When all factors and their interactions are more completely understood, scientists and forest managers will be better able to make choices regarding reforestation and forest management when dealing with climate change.

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APPENDIX A

Analysis of variance (ANOVA) tables for Experiment 1on the influences of light and cold stratification treatments on dormancy breaking and germination for white spruce, black spruce and jack pine seed collections from the Boreal Ecozone in Saskatchewan.

Table A1: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 1).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.05131642	4.93	0.0413
Light	1	0.01217406	1.17	0.2957
Stratification*Light	1	0.13243202	12.71	0.0026

Table A2: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 2).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.10644984	9.08	0.0083
Light	1	0.26307090	22.43	0.0002
Stratification*Light	1	0.01805477	1.54	0.2326

Table A3: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 3).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.07658615	3.56	0.0776
Light	1	0.00310899	0.14	0.7089
Stratification*Light	1	0.16263589	7.55	0.0143

Table A4: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 4).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.02870133	0.99	0.3340
Light	1	0.00721813	0.25	0.6242
Stratification*Light	1	0.04676621	1.62	0.2217

Table A5: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 5).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.00461134	0.42	0.5282
Light	1	0.25464776	22.96	0.0002
Stratification*Light	1	0.00060415	0.05	0.8184

Table A6: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 6).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.14211978	12.64	0.0026
Light	1	0.21756794	19.35	0.0004
Stratification*Light	1	0.26361524	23.45	0.0002

Table A7: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 7).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.06957836	4.50	0.0498
Light	1	0.10435606	6.75	0.0194
Stratification*Light	1	0.09980160	6.46	0.0218

Table A8: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 8).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.02890987	4.48	0.0504
Light	1	0.04393898	6.80	0.0190
Stratification*Light	1	0.00008517	0.01	0.9100

Table A9: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 9).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.35617443	71.40	<.0001
Light	1	0.00153353	0.31	0.5869
Stratification*Light	1	0.00357792	0.72	0.4095

Table A10: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 10).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.12325551	17.96	0.0006
Light	1	0.08302752	12.10	0.0031
Stratification*Light	1	0.00706274	1.03	0.3254

Table A11: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 11).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.00494610	0.19	0.6650
Light	1	0.03071081	1.21	0.2880
Stratification*Light	1	0.03061485	1.20	0.2887

Table A12: ANOVA table for the experiment of stratification and light effects on dormancy breaking for white spruce (collection 12).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.00218449	0.20	0.6617
Light	1	0.00789226	0.72	0.4093
Stratification*Light	1	0.01353000	1.23	0.2837

Table A13: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 1).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.15381891	8.45	0.0103
Light	1	0.01457397	0.80	0.3841
Stratification*Light	1	0.02170153	1.19	0.2910

Table A14: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 2).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.22227548	18.76	0.0005
Light	1	0.01669962	1.41	0.2525
Stratification*Light	1	0.00793247	0.67	0.4253

Table A15: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 3).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.02068276	2.54	0.1308
Light	1	0.01922754	2.36	0.1442
Stratification*Light	1	0.00001439	0.00	0.9670

Table A16: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 4).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.07720135	5.25	0.0358
Light	1	0.00027363	0.02	0.8932
Stratification*Light	1	0.00025005	0.02	0.8979

Table A17: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 5).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.00685300	0.77	0.3945
Light	1	0.00450765	0.50	0.4881
Stratification*Light	1	0.01070091	1.20	0.2904

Table A18: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 6).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.09027391	3.40	0.0837
Light	1	0.00011772	0.00	0.9477
Stratification*Light	1	0.00004146	0.00	0.9690

Table A19: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 7).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.14482754	23.85	0.0002
Light	1	0.00039279	0.06	0.8023
Stratification*Light	1	0.00002769	0.00	0.9470

Table A18: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 8).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.01563557	1.00	0.3311
Light	1	0.03160113	2.03	0.1734
Stratification*Light	1	0.00608993	0.39	0.5405

Table A19: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 9).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.17887980	6.48	0.0216
Light	1	0.02616417	0.95	0.3446
Stratification*Light	1	0.02357927	0.96	0.3409

Table A20: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 10).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.05074628	4.46	0.0508
Light	1	0.00886490	0.78	0.3904
Stratification*Light	1	0.03818914	3.36	0.0856

Table A21: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 11).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.00089950	0.14	0.7135
Light	1	0.01341908	2.08	0.1682
Stratification*Light	1	0.00593070	0.92	0.3516

Table A22: ANOVA table for the experiment of stratification and light effects on dormancy breaking for black spruce (collection 12).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.01267165	0.57	0.4616
Light	1	0.00430676	0.19	0.6660
Stratification*Light	1	0.00243886	0.11	0.7450

Table A23: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 1).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.52957117	51.84	<.0001
Light	1	0.00300154	0.29	0.5953
Stratification*Light	1	0.00124019	0.12	0.7321

Table A24: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 2).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.02304183	2.39	0.1417
Light	1	0.17606151	18.26	0.0006
Stratification*Light	1	0.7205845	7.47	0.0147

Table A25: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 3).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.00365726	0.48	0.4978
Light	1	0.04878869	6.42	0.0221
Stratification*Light	1	0.01664240	2.19	0.1583

Table A26: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 4).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.06647868	5.61	0.0307
Light	1	0.00119035	0.10	0.7553
Stratification*Light	1	0.08009871	6.76	0.0193

Table A27: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 5).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.01847766	3.23	0.0912
Light	1	0.00577190	1.01	0.3301
Stratification*Light	1	0.05143674	8.99	0.0085

Table A28: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 6).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.02364113	2.74	0.1176
Light	1	0.05349496	6.19	0.0242
Stratification*Light	1	0.00195992	0.23	0.6403

Table A29: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 7).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.08108153	10.40	0.0053
Light	1	0.00001421	0.00	0.9665
Stratification*Light	1	0.00673187	0.86	0.3665

Table A30: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 8).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.04810215	5.48	0.0325
Light	1	0.01164420	1.33	0.2663
Stratification*Light	1	0.0567642	0.65	0.4330

Table A31: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 9).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.07099192	6.01	0.0261
Light	1	0.05931687	5.02	0.0395
Stratification*Light	1	0.04653223	3.94	0.0645

Table A32: ANOVA table for the experiment of stratification and light effects on dormancy breaking for jack pine (collection 10).

Source of variation	Degrees of freedom	Type III SS	F	P value
Stratification	1	0.02317182	2.56	0.1290
Light	1	0.22125510	24.47	0.0001
Stratification*Light	1	0.16464127	18.21	0.0006

APPENDIX B

Chapman three model parameters for white spruce, black spruce, and jack pine.

Table C1: Chapman three parameters for white spruce at difference temperatures: a) the asymptote; b) the rate parameter; and c) the shape parameter.

		Collections											
Temperature		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
	a	55.14	28.45	62.72	17.64	43.09	49.04	57.31	52.08	47.65	75.12	43.72	68.60
15ºC	**b**	0.40	0.43	0.34	0.41	0.34	0.51	0.41	0.39	0.35	0.49	0.30	0.39
	c	45.29	114.29	21.07	61.80	37.66	106.56	47.97	46.98	33.31	62.56	17.94	28.14
	a	65.38	83.58	79.30	54.52	76.76	83.47	72.41	85.03	72.81	85.44	80.69	80.35
17.5ºC	**b**	0.53	0.62	0.47	0.44	0.54	0.59	0.76	0.62	0.41	0.60	0.41	0.58
	c	36.88	87.97	30.58	15.93	52.59	54.74	162.12	56.29	16.96	51.41	20.59	41.91
	a	87.02	82.41	80.48	67.35	80.00	85.52	72.94	81.60	73.07	73.71	66.20	72.61
20ºC	**b**	0.65	0.45	0.56	0.46	0.52	0.62	0.60	0.62	0.69	0.67	0.44	0.77
	c	37.36	14.77	21.48	9.75	17.96	25.36	22.63	23.55	39.00	28.34	13.15	42.05
	a	65.20	78.00	63.37	63.50	76.89	87.99	62.45	72.98	39.51	77.21	27.36	48.15
25ºC	**b**	0.47	0.38	0.52	0.30	0.42	0.52	0.38	0.40	0.55	0.50	0.51	0.74
	c	10.89	6.52	14.07	3.87	8.87	11.66	6.59	7.79	14.62	11.62	28.38	25.97
	a	19.53	20.63	16.21	26.47	26.67	35.59	21.77	20.08	13.85	4.61	12.13	11.34
30ºC	**b**	0.22	0.53	0.40	0.19	0.32	0.22	0.30	0.32	0.48	0.85	0.07	0.53
	c	3.11	23.63	19.47	3.26	8.39	3.59	5.64	7.64	10.22	35.95	1.05	10.17

Table C2: Chapman three model parameters for black spruce at difference temperatures: a) the asymptote; b) the rate parameter; and c) the shape parameter.

		Collections											
Temperature		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
	a	27.53	44.31	50.78	76.70	44.17	26.92	58.33	64.06	38.92	73.64	51.03	67.56
15ºC	**b**	0.42	0.43	0.44	0.54	0.29	0.20	0.37	0.61	0.26	0.55	0.23	0.39
	c	169.23	89.42	60.75	160.40	20.97	12.77	35.11	450.72	20.10	169.86	11.14	40.82
	a	91.61	86.69	91.09	86.21	93.26	74.02	99.76	91.00	85.99	89.48	86.48	79.53
17.5ºC	**b**	0.58	0.55	0.54	0.52	0.51	0.28	0.79	0.64	0.40	0.62	0.52	0.66
	c	75.04	62.12	43.75	50.92	34.23	14.29	156.99	84.80	20.92	79.22	41.33	128.10
	a	93.43	97.40	95.39	99.60	97.05	97.27	98.55	99.57	97.28	97.66	87.72	97.15
20ºC	**b**	0.80	0.89	1.15	1.02	0.80	0.78	1.09	1.14	0.83	1.00	0.63	0.90
	c	87.45	111.29	271.49	133.01	77.04	140.95	153.98	268.94	78.08	147.17	30.53	76.92
	a	95.40	94.90	96.70	96.87	99.35	79.71	97.72	98.15	96.29	97.85	79.01	96.84
25ºC	**b**	0.85	1.09	1.48	1.17	0.97	0.65	1.41	1.45	1.29	1.50	0.80	1.12
	c	27.17	75.49	218.47	81.30	47.69	18.60	144.25	183.28	128.46	204.73	21.20	71.67
	a	96.41	97.58	97.00	98.47	98.67	89.30	88.35	95.29	92.91	93.41	81.82	91.93
30ºC	**b**	1.02	1.14	1.32	1.31	1.25	0.84	1.04	1.46	1.11	1.27	0.77	1.21
	c	42.23	59.61	93.28	96.17	105.27	39.34	50.80	149.82	55.48	77.94	16.89	87.94

Table C3: Chapman three model parameters for jack pine at difference temperatures: a) the asymptote; b) the rate parameter; and c) the shape parameter.

		Collections									
Temperature		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
	a	42.55	33.55	18.57	35.99	14.19	19.62	32.17	7.65	43.21	31.75
15ºC	**b**	0.21	0.20	0.38	0.17	0.37	0.34	0.36	0.30	0.31	0.16
	c	10.67	9.89	40.23	5.53	60.82	18.92	45.07	27.14	19.59	3.88
	a	83.35	60.29	99.27	98.76	96.67	98.62	95.32	63.40	97.08	97.56
20ºC	**b**	0.66	0.64	2.14	1.23	1.55	1.63	1.11	0.81	1.12	1.11
	c	43.70	37.43	6423.93	130.09	705.37	867.42	59.75	36.36	65.37	90.13
	a	83.47	63.48	100.01	99.69	94.74	98.32	95.70	76.56	93.69	98.08
25ºC	**b**	1.13	1.13	1.68	1.92	2.08	2.84	1.58	2.28	1.39	1.63
	c	54.05	54.05	102.36	304.47	557.45	4424.47	58.58	1631.79	46.53	84.94
	a	33.09	98.84	98.09	94.82	87.59	97.44	94.91	72.23	82.46	89.82
30ºC	**b**	0.67	1.95	1.97	1.69	1.72	2.35	2.38	1.58	1.47	1.64
	c	4.66	86.37	91.52	55.18	62.86	180.97	175.60	39.13	39.41	59.84
	a	-	74.85	89.08	72.89	38.96	71.95	72.57	20.75	43.19	55.12
35ºC	**b**	-	2.07	1.22	1.31	0.98	1.93	1.17	1.16	1.06	1.37
	c	-	522.97	31.09	30.17	18.13	182.20	23.89	24.22	30.43	80.86

APPENDIX C

Chapman three parameter regression models for each collection of white spruce, black spruce, and jack pine

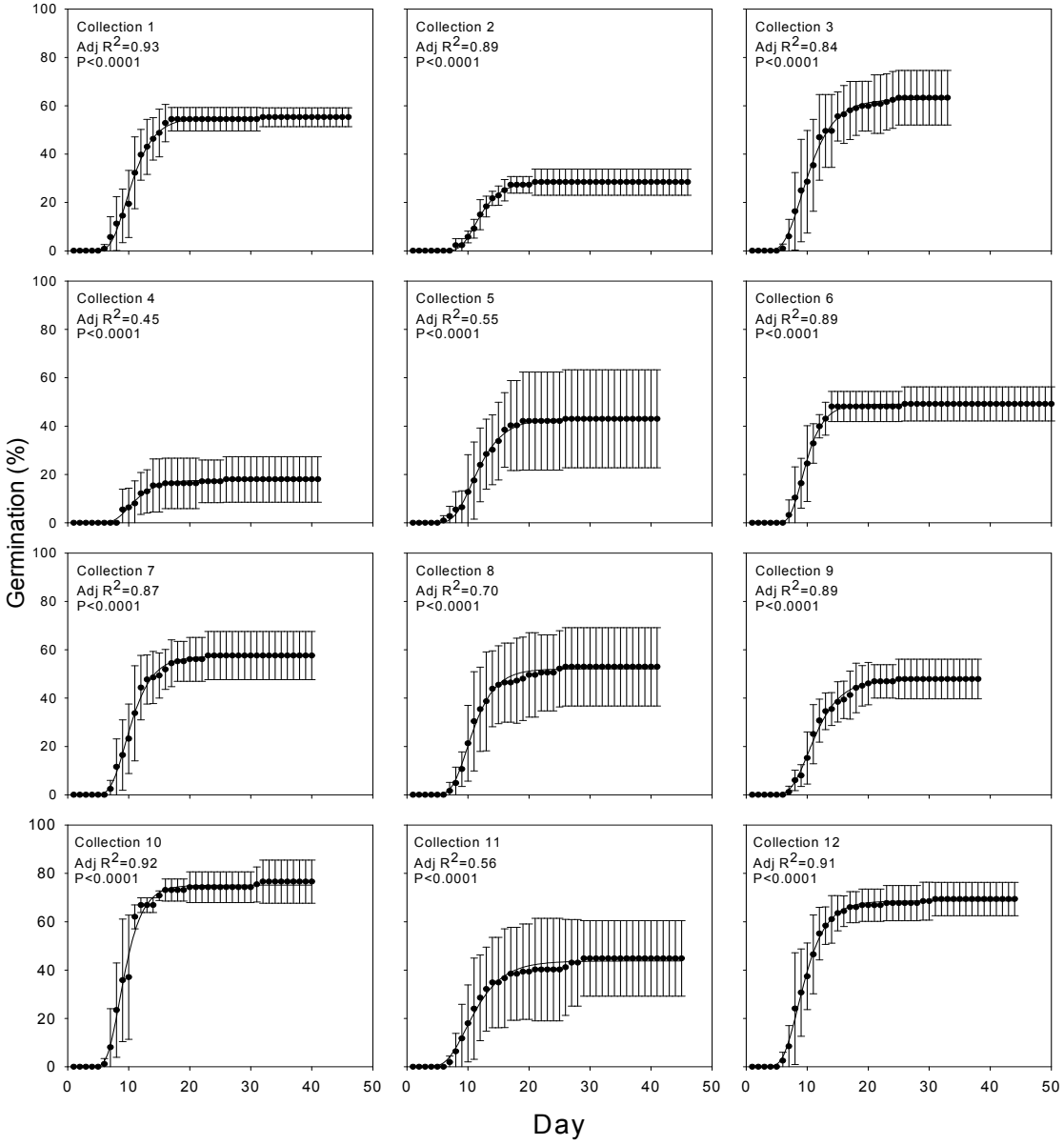

Figure D-1: White spruce Chapman three parameter regressions for temperature 15^{O}C

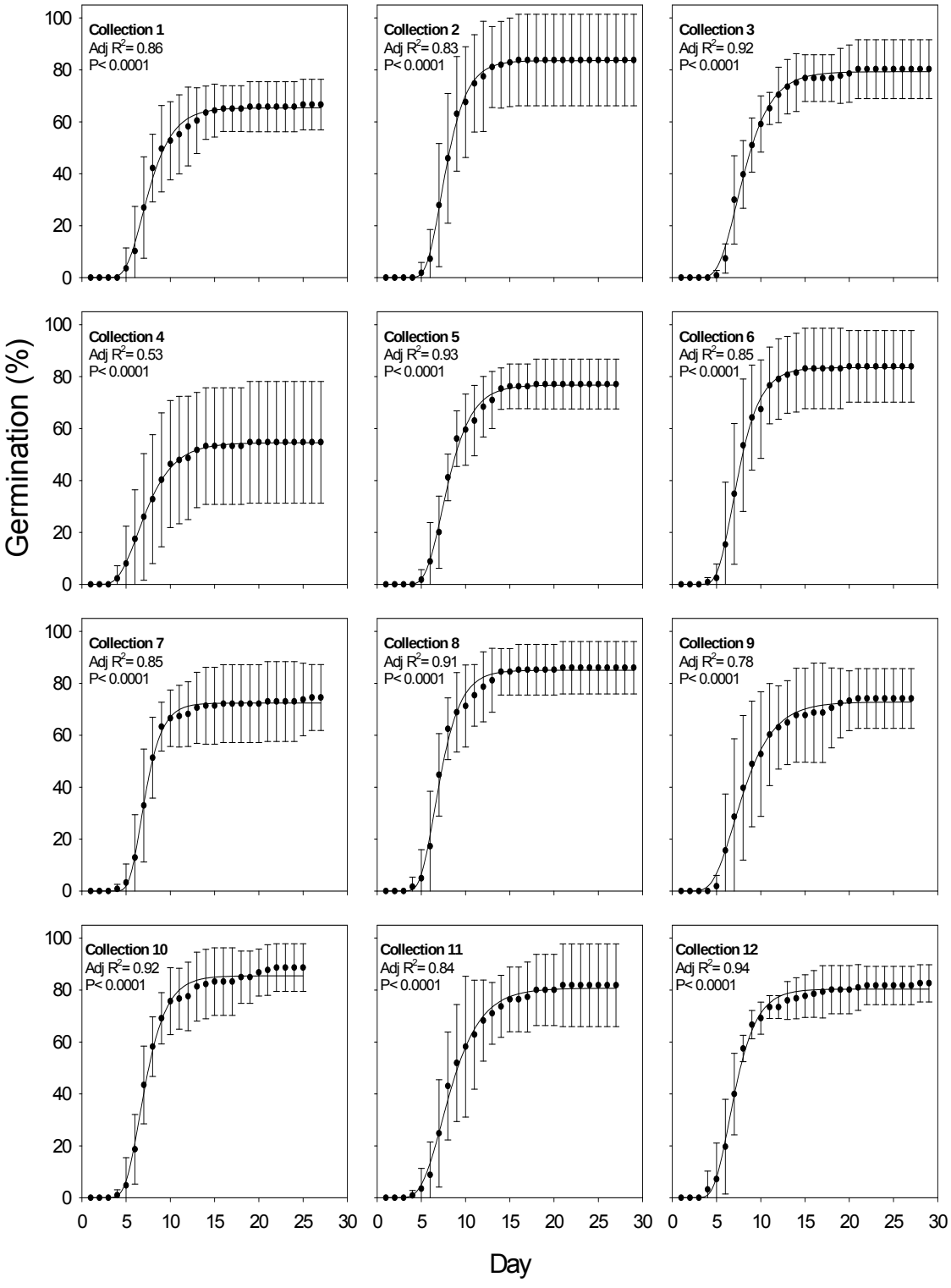

Figure D-2: White spruce Chapman three parameter regressions for temperature 17.5^{O}C

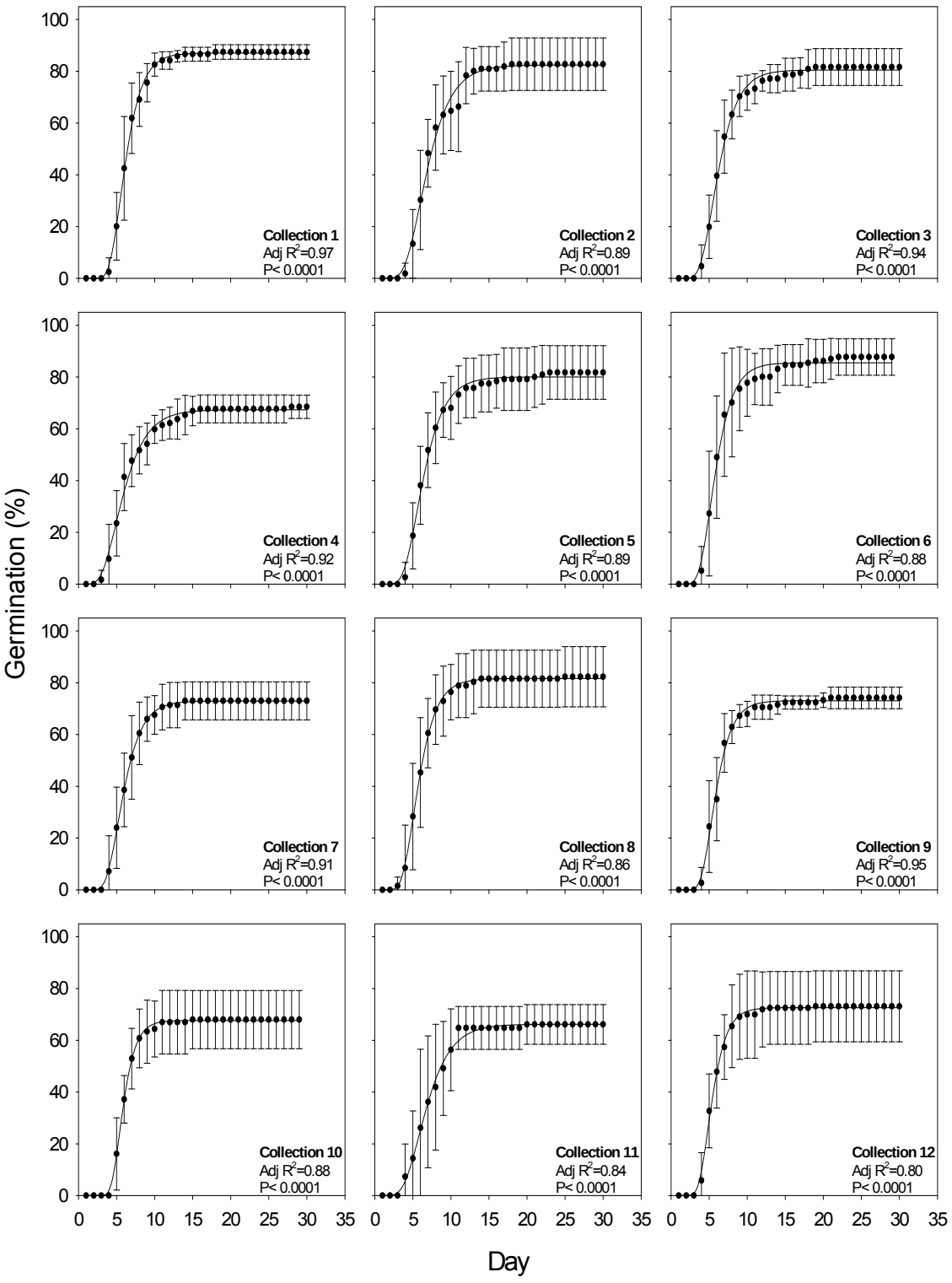

Figure D-3: White spruce Chapman three parameter regressions for temperature 20^{O}C

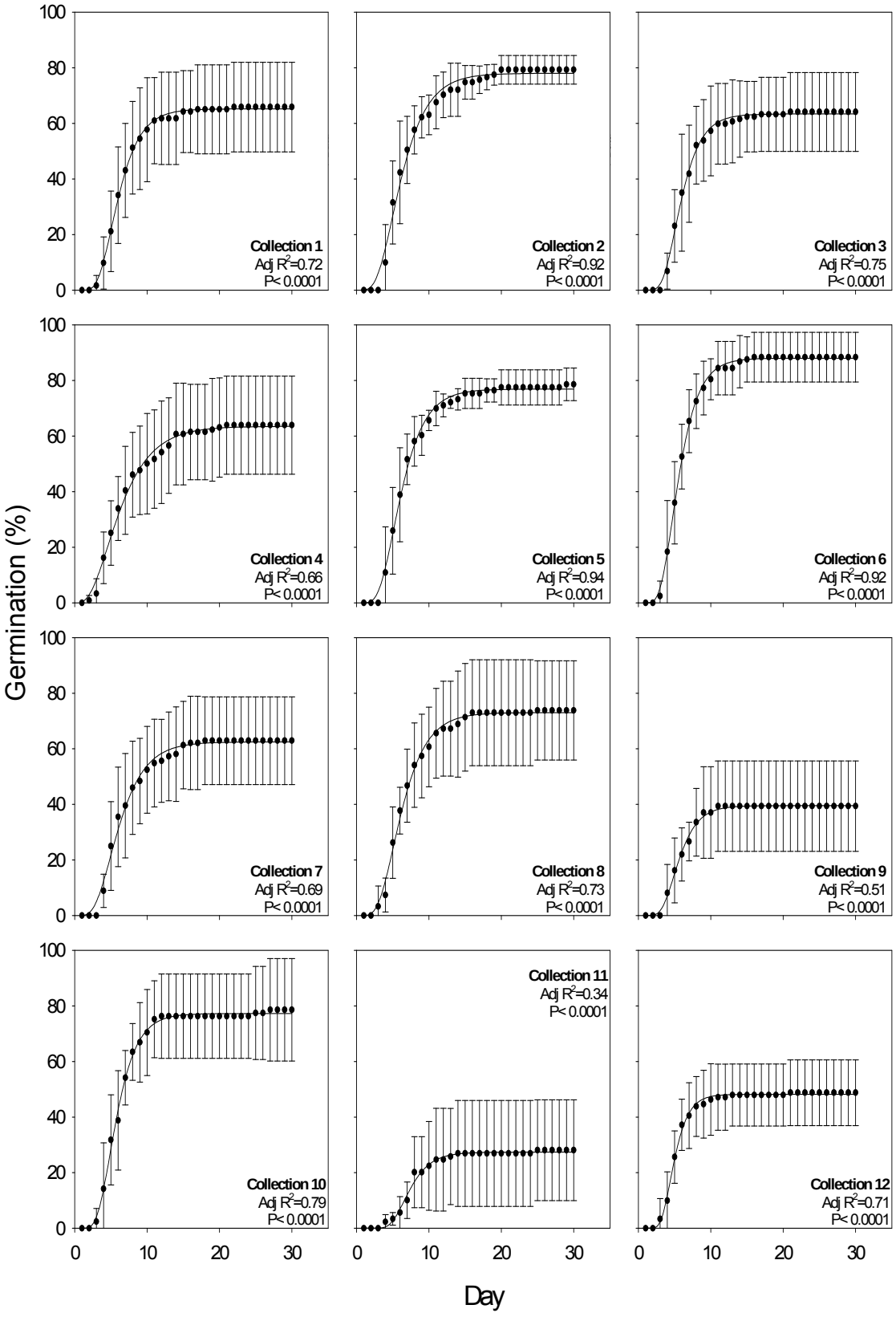

Figure D-4: White spruce Chapman three parameter regressions for temperature 25^{O}C

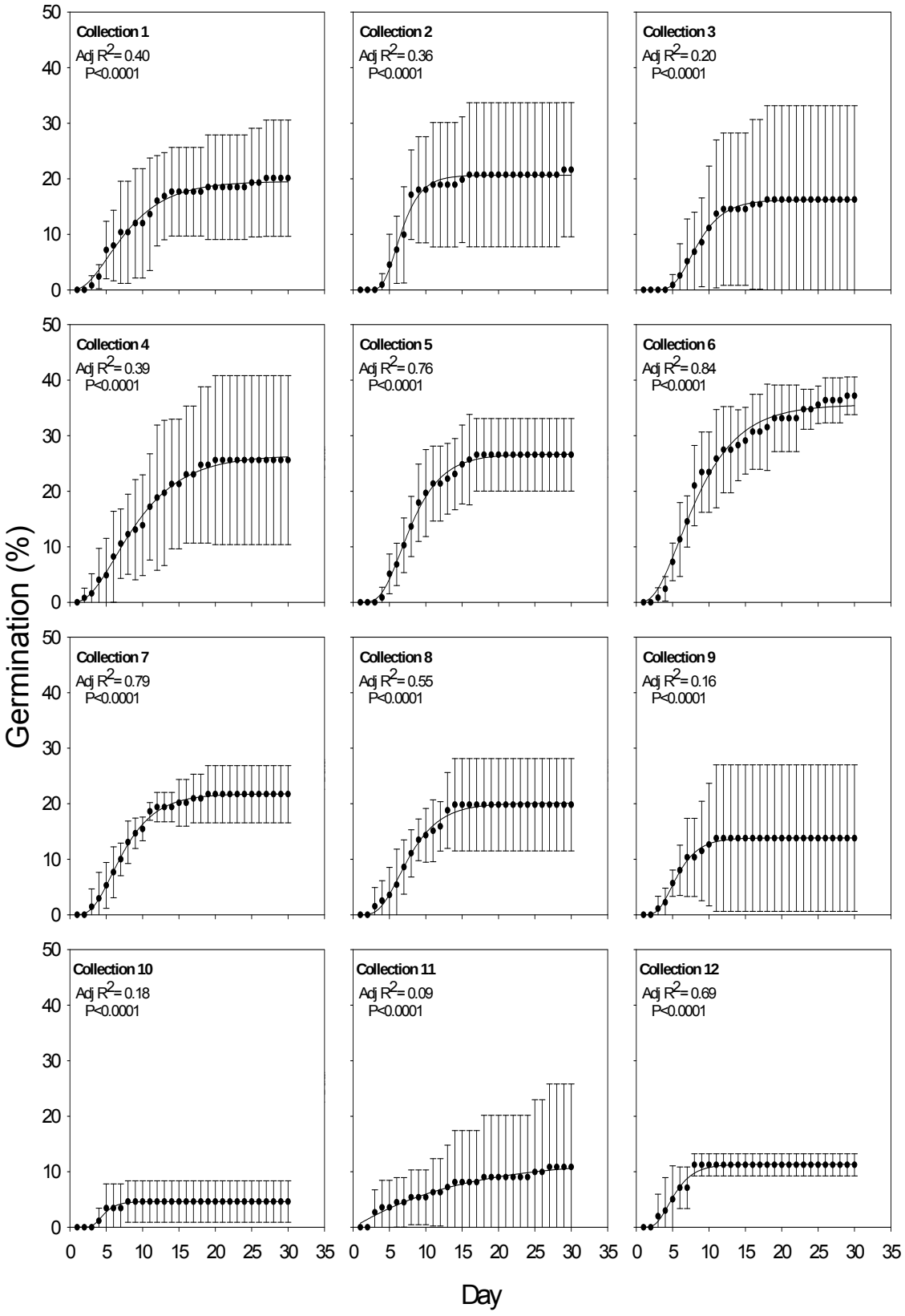

Figure D-5: White spruce Chapman three parameter regressions for temperature 30^{O}C

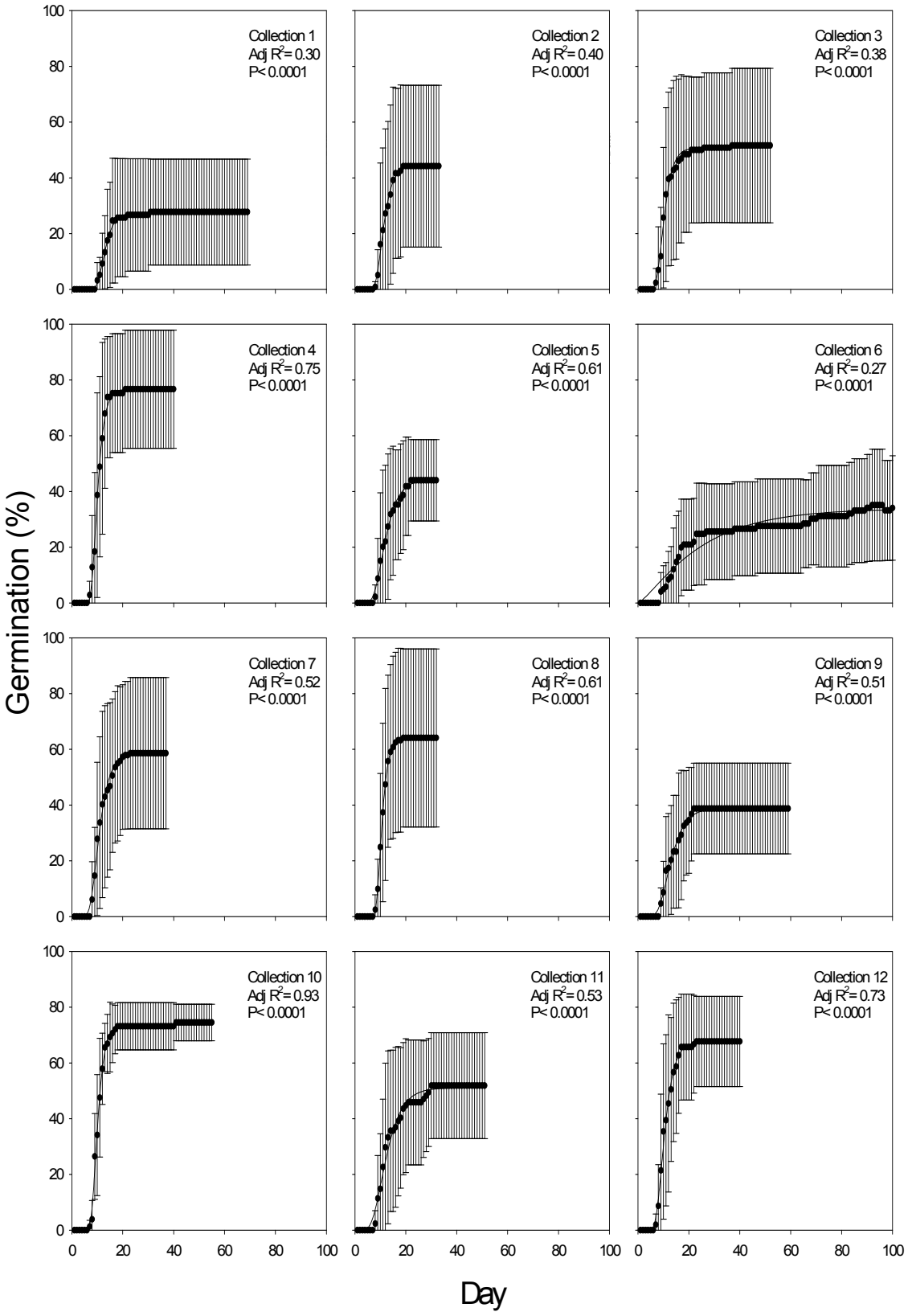

Figure D-6: Black spruce Chapman three parameter regressions for temperature 15^{O}C

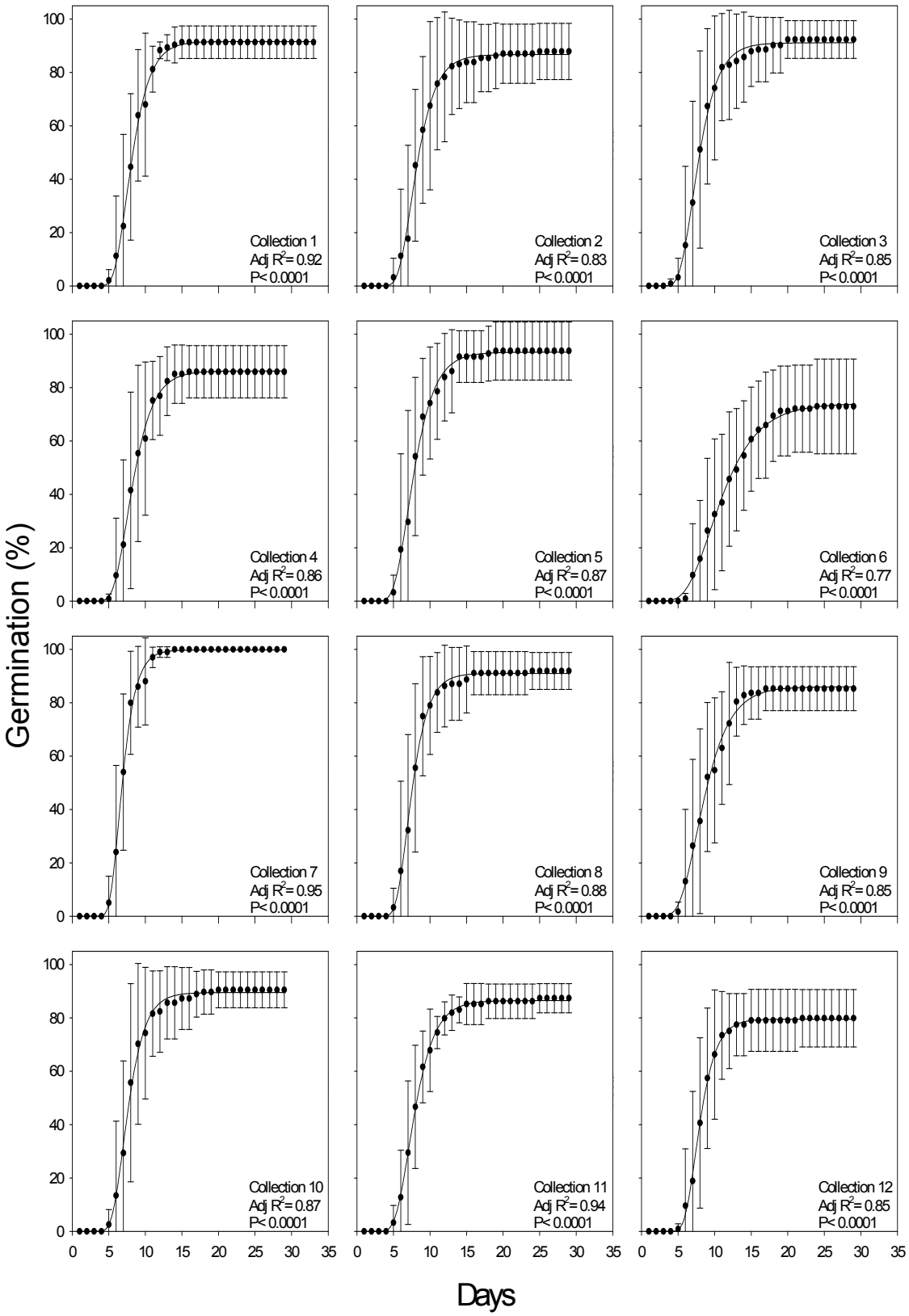

Figure D-7: Black spruce Chapman three parameter regressions for temperature 17.5^{o}C

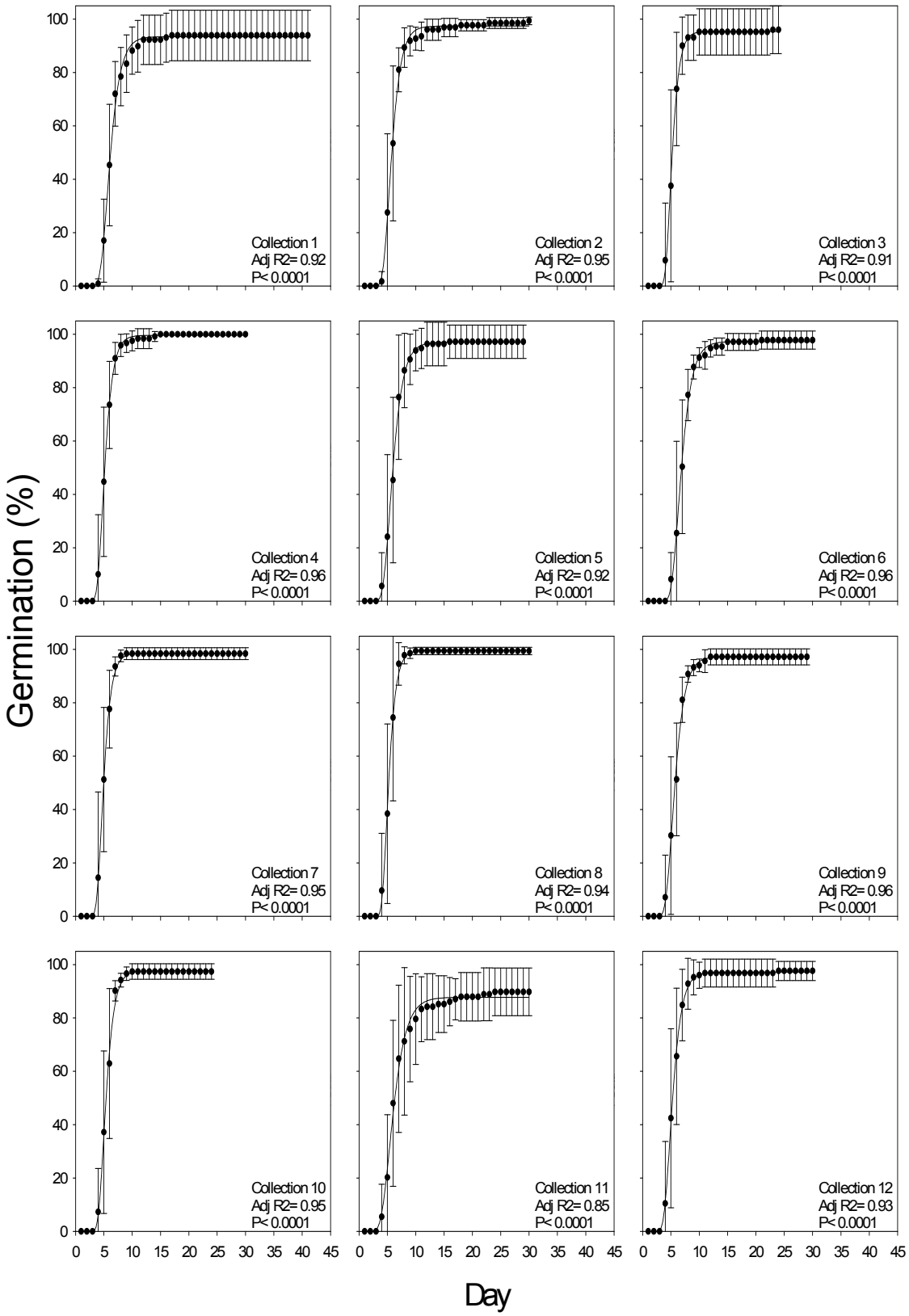

Figure D-8: Black spruce Chapman three parameter regressions for temperature 20^{O}C

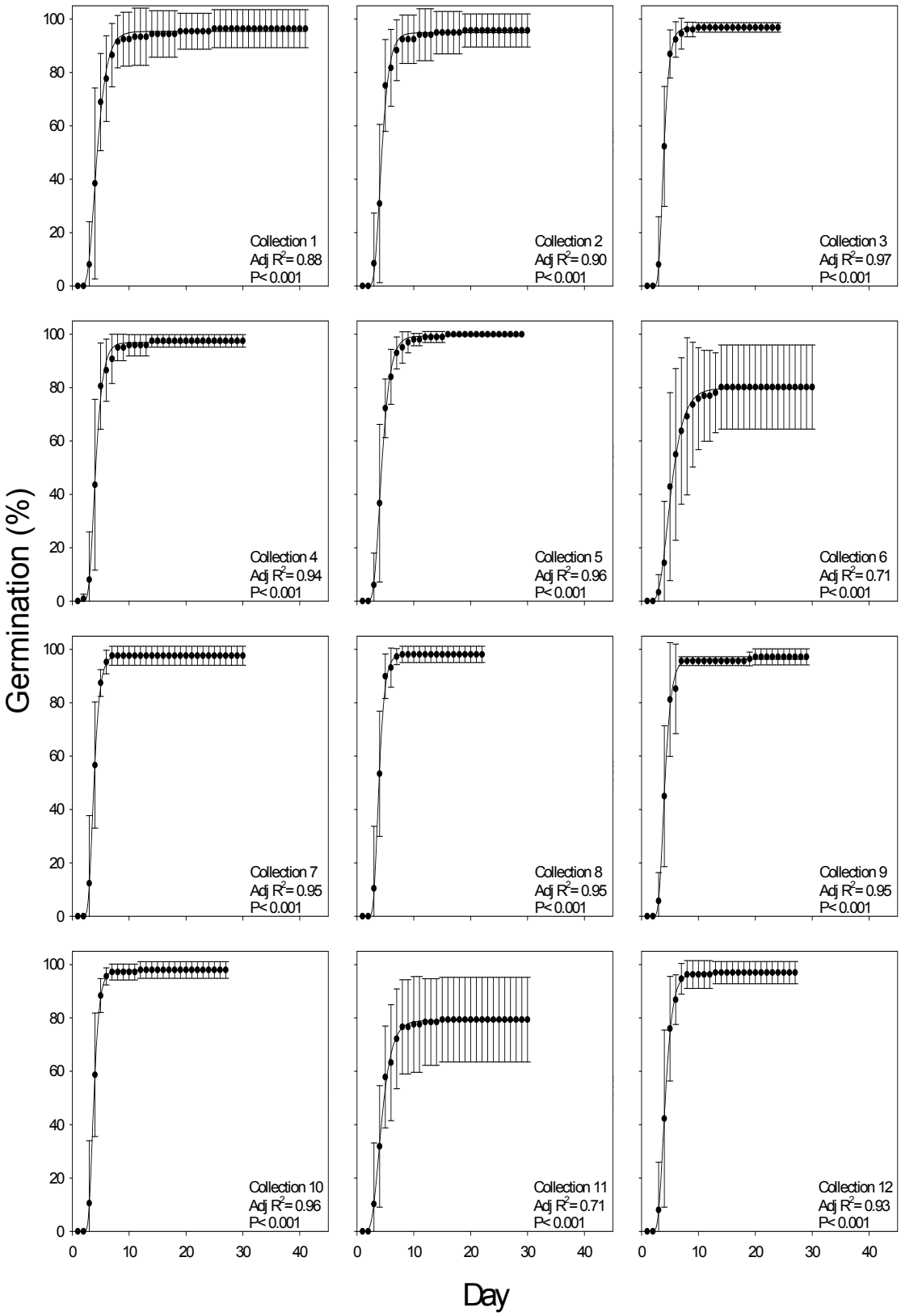

Figure D-9: Black spruce Chapman three parameter regressions for temperature 25^{O}C

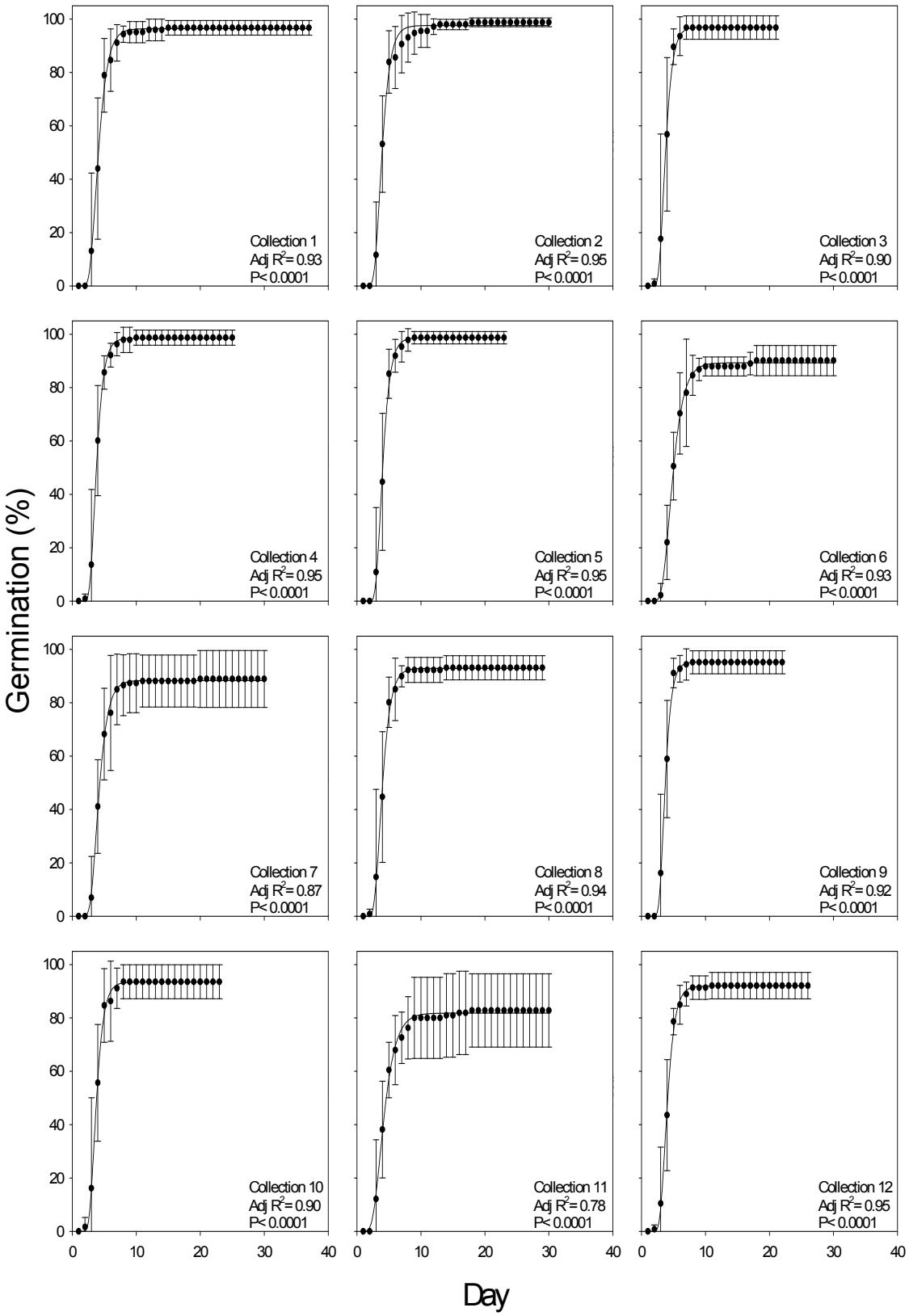

Figure D-10: Black spruce Chapman three parameter regressions for temperature 30^{O}C

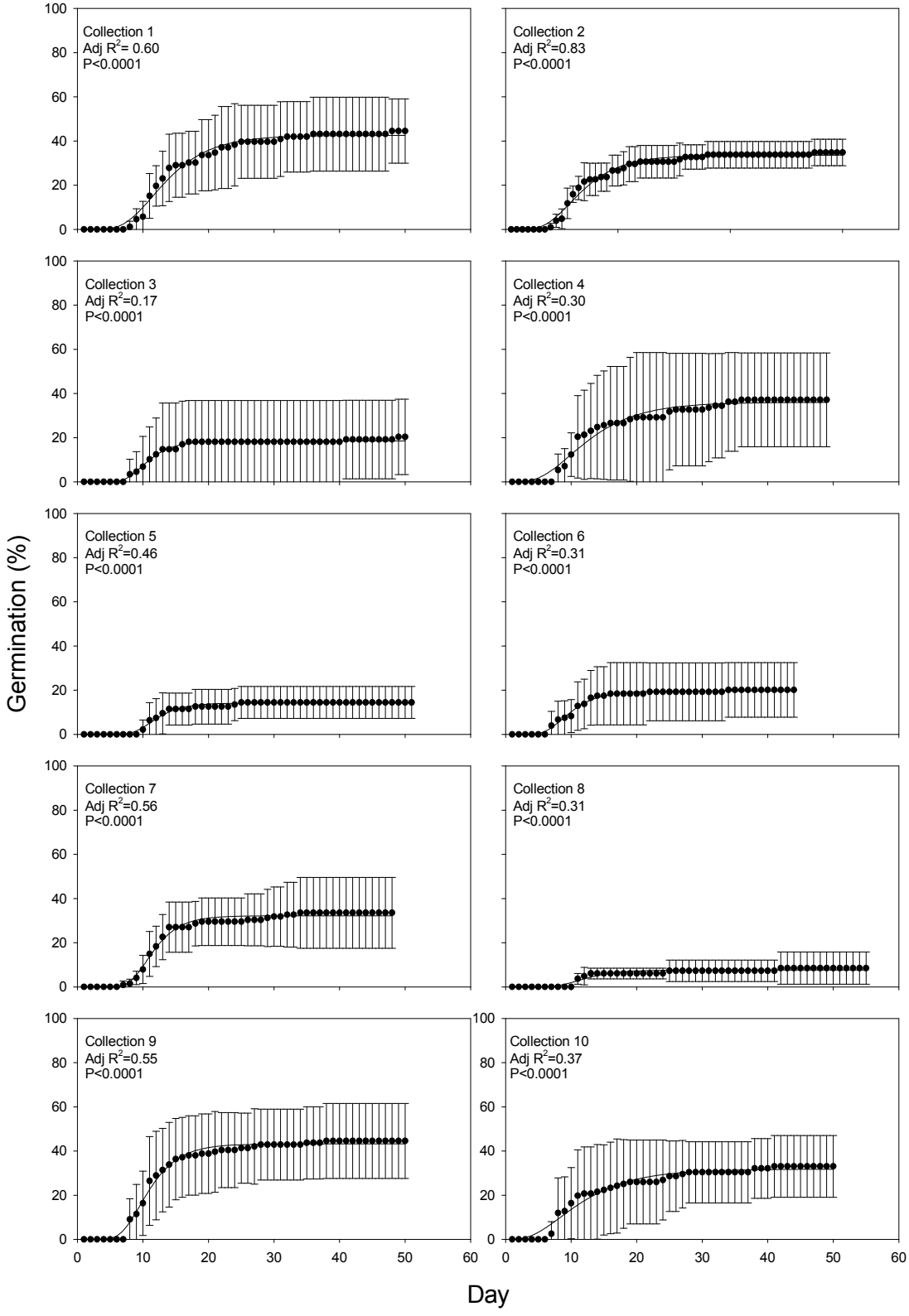

Figure D-11: Jack pine Chapman three parameter regressions for temperature 15^{O}C

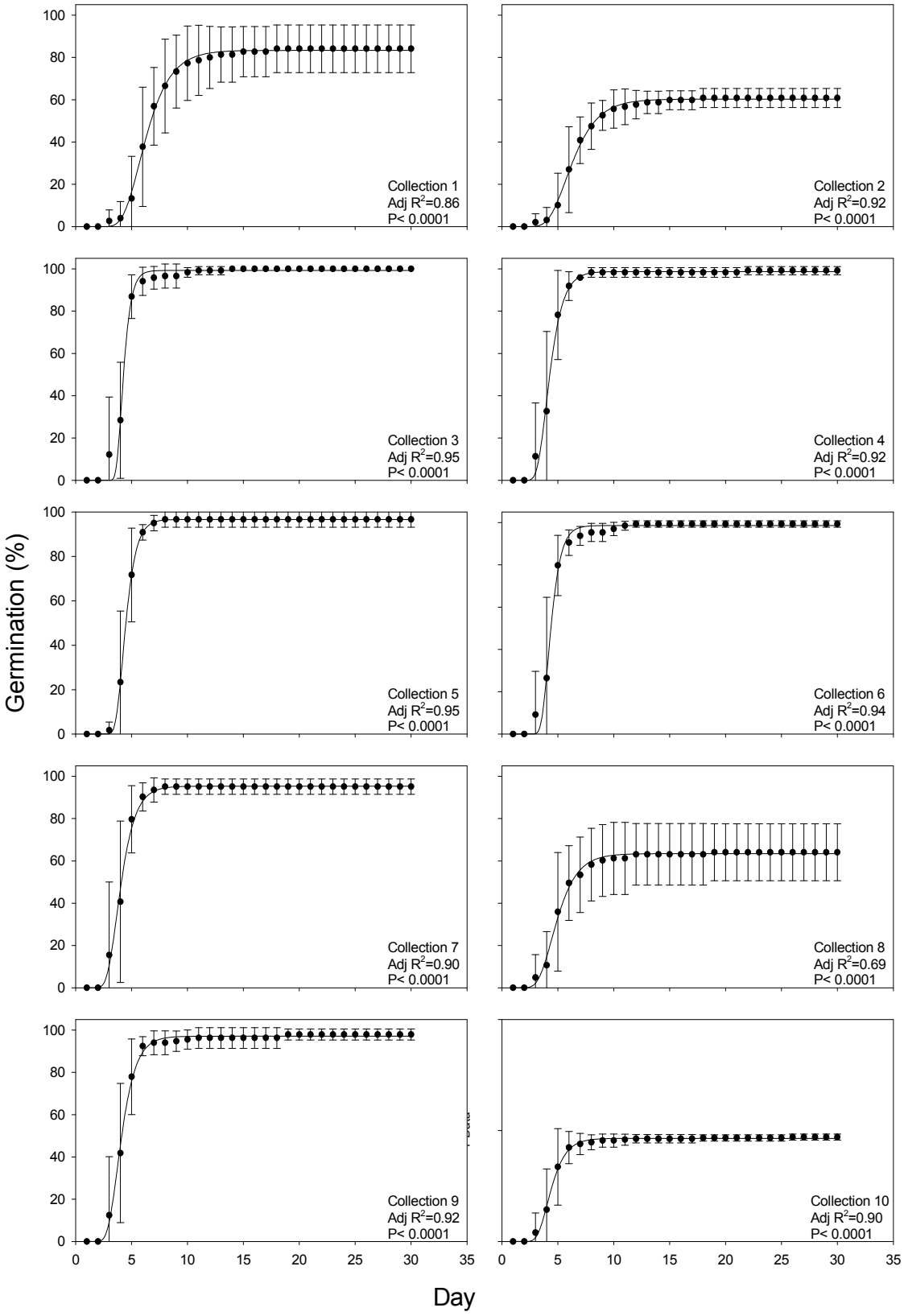

Figure D-12: Jack pine Chapman three parameter regressions for temperature 20^{O}C

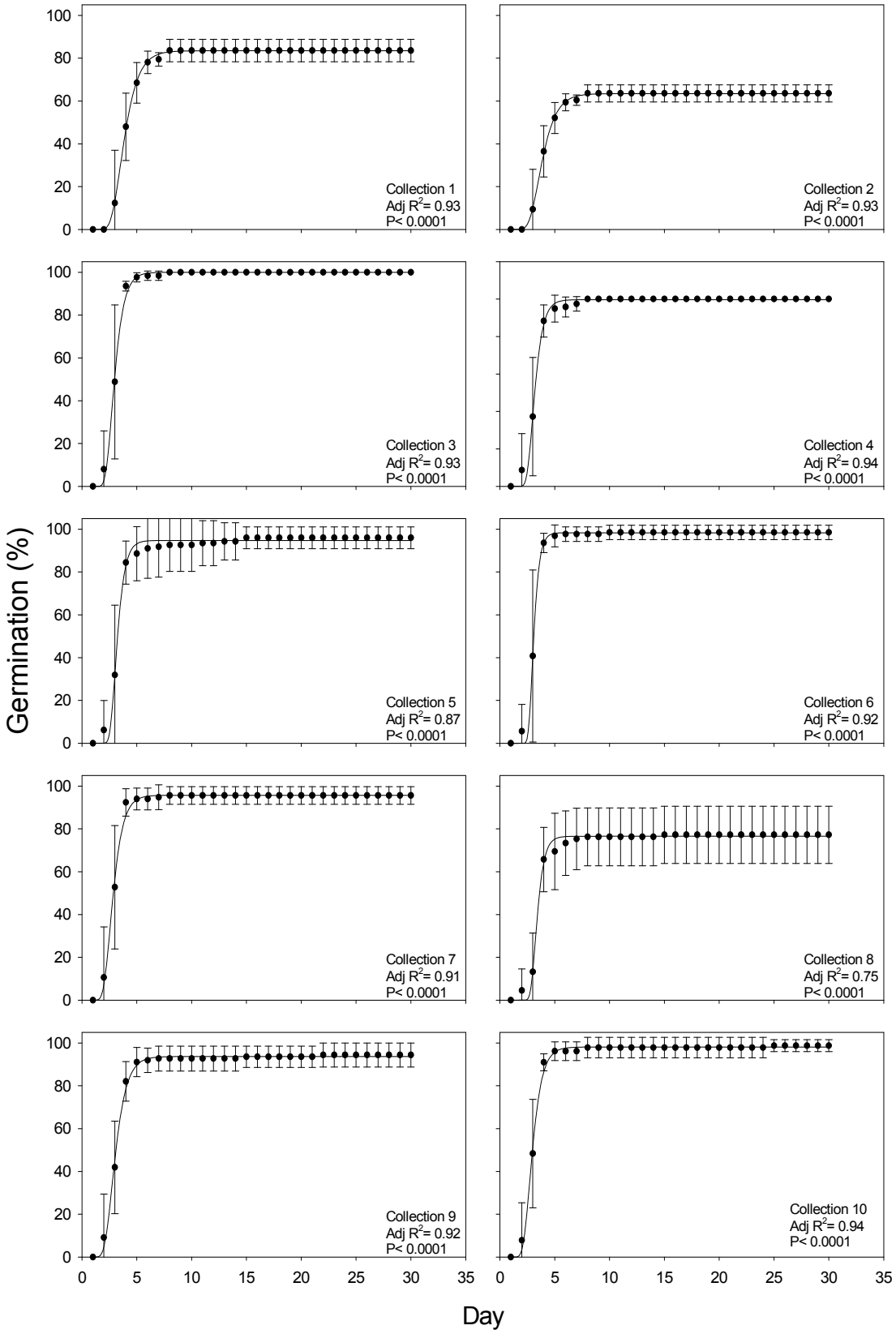

Figure D-13: Jack pine Chapman three parameter regressions for temperature 25^{O}C

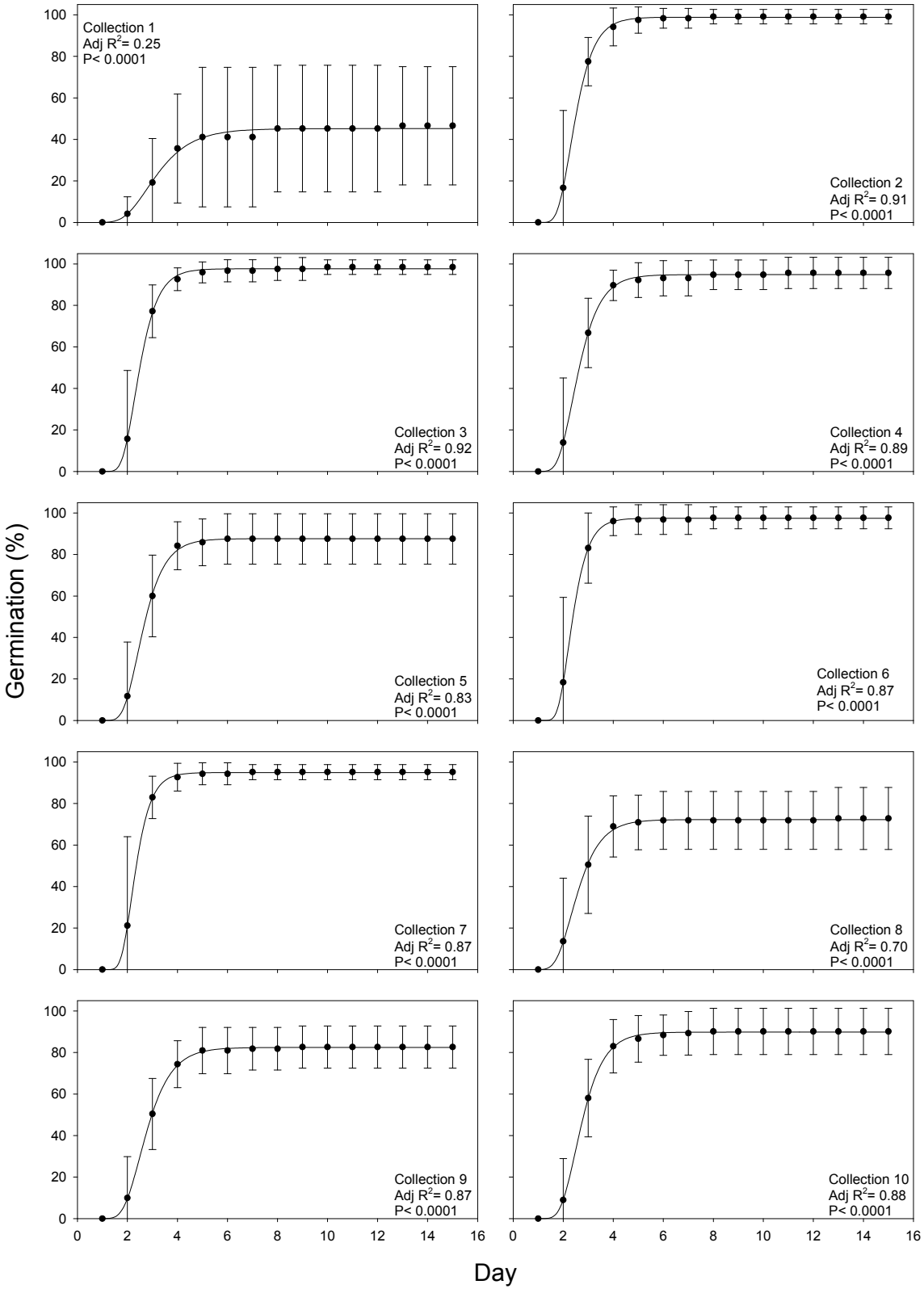

Figure D-14: Jack pine Chapman three parameter regressions for temperature 30^{O}C